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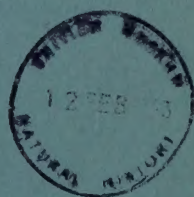
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THE STRUCTURE AND
RELATIONSHIPS OF
THE JURASSIC FISH
ICHTHYOKENTEMA PURBECKENSIS

J. GRIFFITH
AND
C. PATTERSON



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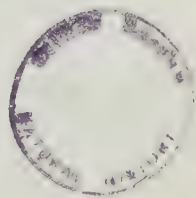
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Pp. 1-43 ; 4 Plates ; 14 Text-figures



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THE STRUCTURE AND RELATIONSHIPS OF THE JURASSIC FISH

ICHTHYOKENTEMA PURBECKENSIS

BY JOHN GRIFFITH AND COLIN PATTERSON

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SYNOPSIS

Ichthyokentema purbeckensis (Davies), a halecostome from beds of marine or hypersaline origin in the lower half of the Purbeck, is described in detail. The species differs from known members of the Pholidophoridae in a number of characters, especially in the structure of the snout, and a new family Ichthyokentemidae is made to contain it. Variations in the structure of the snout in halecostomes are shown to separate the group into at least two lines which may be only distantly related. The origin of the halecostomes is to be found near the Parasemionotidae, but it is considered that the parasemionotids are unlikely to have been directly ancestral to the group because of the structure of their neurocrania. The evolution of the fossa bridgei is discussed, and it is concluded that the post-temporal fossa of holosteans and teleosts is not homologous with the fossa bridgei, but is a new structure which has replaced the latter.

I. INTRODUCTION

IN 1958 and 1959 the authors and Dr. B. G. Gardiner collected a large number of disarticulated fish bones from the Lower Purbeck Broken Beds near Lulworth Cove, Dorset. The bulk of this material has proved to belong to *Ichthyokentema purbeckensis*

(Davies), a species previously known by about a dozen complete but crushed specimens. The new material has enabled us to produce an almost complete description of the species. *Ichthyokentema* is found to differ in some important respects from *Pholidophorus*, to which it was thought to be closely related, and these differences have led us to form some new opinions on the origin and evolution of the halecostomes.

The classification used is that of Arambourg & Bertin (1958), in which the "holosteans" are divided into two super-orders, Holostei and Halecostomi, the latter being further divided into the orders Pholidophoriformes, Leptolepiformes and Aspidorhynchiformes.

II. MATERIAL AND CONDITIONS OF DEPOSITION

The material on which this account is based consists of the British Museum (Natural History) collection of *Ichthyokentema purbeckensis* together with the new material of this species collected in Dorset and since added to the British Museum collection.

The new material consists of several hundred specimens collected from the Broken Beds near Lulworth Cove. The Broken Beds contain up to 15 ft. of fissile, sandy limestone which have become shattered and deformed into a coarse breccia. The processes responsible for this deformation are discussed by Arkell (1938) and Hollingworth (1938). The conclusion reached by these authors is that the Broken Beds result from Tertiary tectonic action on beds previously weakened by the solution of gypsum. This has been confirmed by the proving of gypsum *in situ* at the horizon of the Broken Beds in boreholes below the Weald.

At Lulworth there is a 6-in. band of yellow-brown, sandy limestone, darker in colour than the surrounding purer limestone, lying about 6 ft. 3 in. below the top of the Broken Beds. Eight inches below this band there is a similar band, 3 to 5 in. thick. The fishes were found in the 3 ft. 6 in. of limestone directly below this band. The specimens were collected from a single large block, about 10 ft. long and 4 ft. thick, lying immediately above the "fossil forest" where it is exposed in the cliff a quarter of a mile east of the mouth of Lulworth Cove. The bones were distributed throughout 3 ft. 6 in. of sediment, and were common everywhere, though more abundant in and near the clay partings which occur irregularly in the rock. The fish remains are all disarticulated, only the neurocrania, mandibles and pectoral girdles being preserved reasonably intact. Though the bones lie scattered throughout the rock, they are perfectly preserved, and show no signs of rolling or abrasion. There are some signs that the bones have been water sorted, for while no specimen shows scattered remains of a single skeleton, it is common to find two or three neurocrania lying close together with no other bones in their vicinity. The vast majority of the bones are of *Ichthyokentema purbeckensis*: we have parts of at least 50 neurocrania of this species. A few fragments of other fishes are present, including a maxilla, a preoperculum, a hyomandibular, a dentary, an angular, vertebrae and scales of a leptolepid, scales and teeth of a holostean and some undetermined teeth. Associated with the fishes are fragmentary plant remains and abundant ostracods

of the two species "*Cypris*" *purbeckensis* Forbes and *Fabanella bononiensis* (Jones) (= *Candona bononiensis*), with the former more abundant.

The British Museum collection contains eleven specimens of *Ichthyokentema purbeckensis* including the holotype and three specimens in counterpart. All the specimens are complete fishes, not fragments like the Lulworth material, and all are from the Purbeck beds, though the precise horizon and locality are recorded for very few. The holotype, P. 6171, is from the Lower Purbeck of the Isle of Portland, and two other specimens, 40635 and P. 12515 are from the same horizon and locality. P. 7640 is from the Lower Purbeck "White Lias" of the Teffont Lime Kiln quarry, Teffont Evias, Wilts. There are three bands of "White Lias"—a hard, white marl—at Teffont, all in the Lower Purbeck (Woodward, 1895 : 271), and the exact horizon of the specimen is therefore unknown, but the British Museum collection includes specimens of *Leptolepis brodiei*, *Pleuropholis formosa* and *Ceramurus macrocephalus* from the same rock at this locality, and the holotype of *P. formosa*, P. 10986, is labelled as being from the second band of "Lias", which lies near the base of the Lower Purbeck, at the same horizon as the Broken Beds. The only other fossils contained in this "White Lias" matrix are minute bodies which Dr. F. W. Anderson suggests are algal fragments. P. 1074, the holotype of *Pholidophorus brevis* Davies (shown below to be a synonym of *I. purbeckensis*) and P. 1073/3607, a specimen in counterpart previously referred to *P. brevis*, are both labelled as being from the Upper Purbeck of Upway, near Weymouth, but Strahan (1898 : 108) describes Upway as showing Lower Purbeck beds only, and the matrix of the specimens appears identical with that in the Broken Beds, suggesting that the specimens are in fact from the Lower Purbeck. This has been confirmed by Dr. F. W. Anderson, who has identified the typical Lower Purbeck ostracods "*Cypris*" *purbeckensis* and *Fabanella bononiensis* in the matrix. Of the remaining five specimens, P. 8378 and P. 8379 are from the Purbeckian of the Isle of Portland, P. 12347 is from the Purbeckian of Swanage, and P. 7640 and P. 7807 are of unknown provenance. With the exception of the specimen from Teffont and P. 12347, all the specimens are in matrices which appear identical with the Broken Beds, with plant fragments and "*Cypris*" *purbeckensis*. P. 12347 is in a crystalline, shelly limestone: the shells are of bivalves, but are too poorly preserved for identification. In this matrix Dr. Anderson has identified one specimen of *Cypridea granulosa* (Sowerby), an ostracod characteristic of brackish water facies in the lower part of the Middle Purbeck. Dr. Anderson places the specimen at a horizon about 12 ft. below the Cinder bed. The known range of *I. purbeckensis* is thus from the base of the Lower Purbeck to the lower part of the Middle Purbeck.

The ostracods "*Cypris*" *purbeckensis* Forbes and *Fabanella bononiensis* (Jones), previously thought to be freshwater forms (Arkell, 1933 : 534), are now known to be typical of a marine or hypersaline facies (Anderson, 1958 : 128). The Broken Beds, containing gypsum and a very limited fauna of ostracods and fish, with no molluscs, obviously represent a hypersaline facies, and must have been laid down in a partially or completely enclosed body of salt water in which the salt concentration was raised periodically or maintained at a high level by evaporation. All but two of the known specimens of *I. purbeckensis* come from this type of deposit, suggesting that the

species was marine, though the possibility of the fish having been washed into the body of salt water with an influx of fresh water is not completely excluded. The other two matrices from which the fish is known do not give definite confirmation of a marine habitat; the "White Lias", with no other fossils except algal fragments, is obviously representative of a specialized habitat, neither purely freshwater nor marine, while the shelly matrix of P. 12347 with a single specimen of the brackish water ostracod *Cypridea granulosa* (Sowerby) indicates a brackish water deposit. The absence of the species from any of the freshwater deposits of the Purbeck tends to confirm that the habitat was marine. The balance of the evidence indicates that *I. purbeckensis* was a marine fish, possibly adapted to hypersaline conditions. The association of *Leptolepis brodiei*, *Pleuropholis formosa* and *Ceramurus macrocephalus* with *Ichthyokentema purbeckensis* in the "White Lias" at Teffont suggests that these three species were also marine.

III. METHODS

The new material from Lulworth was prepared mainly by dissolving the matrix with dilute acetic acid. Attempts were made both with the British Museum material and the new material to embed specimens in resin and remove the matrix with acid, but the rock proved too marly for this method to give good results. The scales removed from the Lulworth matrix were too friable for satisfactory sectioning, but excellent preparations were made by washing the dried scales in xylene and mounting in Naphrax: when examined in transmitted light these preparations show the structure of the scales very clearly (Pl. 2, fig. 6). Text-figures 1, 6 and 7 are based on photographs of a plasticine model on to which enlarged outlines of the individual bones were fitted. All specimens are referred to by their registered numbers in the British Museum (Natural History). Numbers in the series P. 44923-79 and P. 45020-39 refer to the new material from Lulworth, other numbers refer to older specimens.

IV. DESCRIPTION

Super-Order HALECOSTOMI. For diagnosis see Arambourg & Bertin, 1958 : 2195
Order PHOLIDOPHORIFORMES

For diagnosis see Berg, 1940: 214 but add "maxilla with one or two supramaxillae" and delete "mandible without coronoids".

Family ICHTHYOKENTEMIDAE nov.

DIAGNOSIS. Small, fusiform Pholidophoriformes; the bones of the head and scales ganoine covered but not strongly ornamented; a toothed rostral separating the premaxillae; nasals broadly in contact in the mid-line; supraorbital sensory canal ending in the parietal and having no anastomosis with the infraorbital canal, anterior and middle pit-lines on the parietal, the latter extending on to the dermopterotic; neurocranium ossified in separate bones, but some fusion in the otic region in the adult, ethmoid region a single ossification, interorbital septum poorly ossified, no aortic groove or canal below the occipital condyle, lateral wall of jugular canal very weakly ossified, basisphenoid pedicel with a pair of canals for the internal carotids, vomer unpaired; dermosphenotic elongated dorso-ventrally,

second infraorbital below the dermosphenotic enlarged and bearing horizontal and vertical pit-lines ; a single suborbital ; four supraorbitals ; suspensorium slightly inclined forwards ; a single supramaxilla ; mandible with dentary, articular, a fully ossified Meckel's cartilage and a single coronoid, oral pit-line present on articular ; teeth borne on rostral, premaxilla, maxilla, vomer, parasphenoid, endopterygoid, dentary and coronoid ; a single gular ; preopercular not expanded at the angle, suture between opercular and subopercular almost horizontal ; vertebrae with annular centra, notochord almost unconstricted, neural and haemal arches fused with centra, ribs articulating with short transverse processes, no epipleurals or epineurals ; suprascapular large, endoskeletal pectoral girdle ossified in a single piece, mesocoracoid arch present ; large fulcra present on all fins ; scales rhomboid, with bone cells and canals of Williamson, hind edge not pectinated, the single lateral line passing through a row of deepened scales on the flank.

Genus *ICHTHYOKENTEMA* A. S. Woodward, 1941 : 90.

DIAGNOSIS. As for family (only genus).

TYPE SPECIES. *Pholidophorus purbeckensis* Davies.

Ichthyokentema purbeckensis (Davies)

(Pls. 1-4 ; Text-figs. 1-14)

- 1887. *Pholidophorus purbeckensis* Davies, p. 337, pl. 10, figs. 2-4.
- 1887. *Pholidophorus brevis* Davies, p. 338, pl. 10, fig. 1.
- 1888. *Pholidophorus purbeckensis* Davies : Davies in Damon, p. xix, pl. 19, fig. 1.
- 1895. *Pholidophorus purbeckensis* Davies : A. S. Woodward, p. 460.
- 1919. *Pholidophorus purbeckensis* Davies : A. S. Woodward, p. 108, pl. 22, figs. 1-3.
- 1919. *Pholidophorus brevis* Davies : A. S. Woodward, p. 110, pl. 22, figs. 4, 5.
- 1941. *Ichthyokentema purbeckensis* (Davies) A. S. Woodward, p. 90.
- 1941. *Ichthyokentema brevis* (Davies) A. S. Woodward, p. 90.

A. S. Woodward (1895 : 460) considered *Pholidophorus brevis* Davies to be a synonym of *P. purbeckensis*, but later (1919 : 110) he reinstated the species, finding it to be "shorter and stouter" than *P. purbeckensis* and to come from the Upper Purbeck, while *P. purbeckensis* ranged from the Lower to Middle Purbeck. It is shown above, however, that the specimens referred to *P. brevis* are in fact from the Lower Purbeck. We have been able to find no characters by which these specimens may be differentiated from *I. purbeckensis*, and are of the opinion that *I. brevis* is a synonym of *I. purbeckensis*.

EMENDED DIAGNOSIS. A species of *Ichthyokentema* reaching about 7 cm. in standard length, length of head slightly greater than maximum depth of trunk and equal to about three-tenths of the standard length ; fin formula : P.11+ ; V.5+ ; D.9 ; A.6-7 ; C.19 ; ten or eleven scales in each transverse series on the trunk, about thirty-five scales along the lateral line, lateral line scales up to four times as deep as long.

HOLOTYPE. British Museum (Natural History) No. P. 6171.

(a) *Measurements and Proportions*

Measurements of the more complete specimens are given in Table I and a photograph of P. 8378 is shown in Pl. 1, fig. 1. The specimens are small, most of them having a total length of between 6 and 8 cm. Roughly 30 per cent of the total length is occupied by the head and the maximum depth of the trunk is equal to nearly the same fraction of the total length. The fins are of moderate size. The pelvic fins lie a little nearer to the tip of the snout than to the fork of the caudal fin. The dorsal and anal fins are triangular and of approximately equal size; the dorsal commences a short distance behind the level of the pelvics and the anal a little further back still. The caudal fin, which is moderately deeply forked, is of hemiheterocercal type.

While it is impossible to obtain measurements of the individuals from which the fragmentary material from Lulworth is derived, the fragments themselves are similar in size to the corresponding parts of the more complete specimens.

TABLE I

(All measurements in mm.)

Specimen No.	Tip of snout to fork of caudal fin	Tip of snout to origin of anal fin	Length of skull (including operculum)	Maximum depth of trunk
P. 7640 . . .	c 44 .	27.5 .	12 .	11.5
P. 8378 . . .	64 .	40 .	c 18.5 .	17
P. 12515 . . .	67 .	42 .	19.5 .	17
P. 8379 . . .	c 68 .	c 45 .	c 19.5 .	17
P. 7807 . . .	71 .	47 .	c 20.5 .	18
40635a . . .	76 .	53 .	— .	20.5
P. 3607, P. 1073	— .	52 .	23 .	23.5
P. 1074 . . .	64 .	43 .	18 .	23
P. 6171 . . .	c 68 .	c 43 .	— .	20

(b) *Neurocranium and Skull Roof*

The skull roof is shown in Text-fig. 1 and Pl. 2, fig. 3, and lateral, ventral and posterior views of the reconstructed neurocranium are shown in Text-figs. 2 to 4. Pl. 3, figs. 7, 8 show stereoscopic pairs of the neurocranium in ventral view and the cranial cavity in dorsal view.

The neurocranium is long, and only about two-thirds as deep as it is broad. The orbit is large, and the interorbital septum is very incompletely ossified. The neurocranium is well ossified, with few cartilagenous interspaces in its walls. The sutures between the cartilage bones are often indistinguishable on the external surface of the neurocranium, but they can usually be recognized on the internal surface of the bones.

The dermal roof of the skull is flat, and gently rounded in the transverse plane. The parietal (pa.) is about as large as it is in *Pholidophorus similis* (Saint-Seine, 1949: 216) and is a rectangular bone, meeting its fellow in the mid-line, the frontal anteriorly, the dermopterotic laterally, and overlying the epiotic and supraoccipital. The parietal bears the anterior pit-line, the medial part of the middle pit-line, and, in most specimens, the terminal part of the supraorbital sensory canal. The bone is ornamented with a few weak ridges radiating from its postero-medial corner.

The frontal (fr.) is the usual very large bone, meeting its fellow in the mid-line and the parietal and dermopterotic posteriorly. Above the orbit the lateral edge of the frontal is perfectly smooth, and shows no signs of the articulation of the

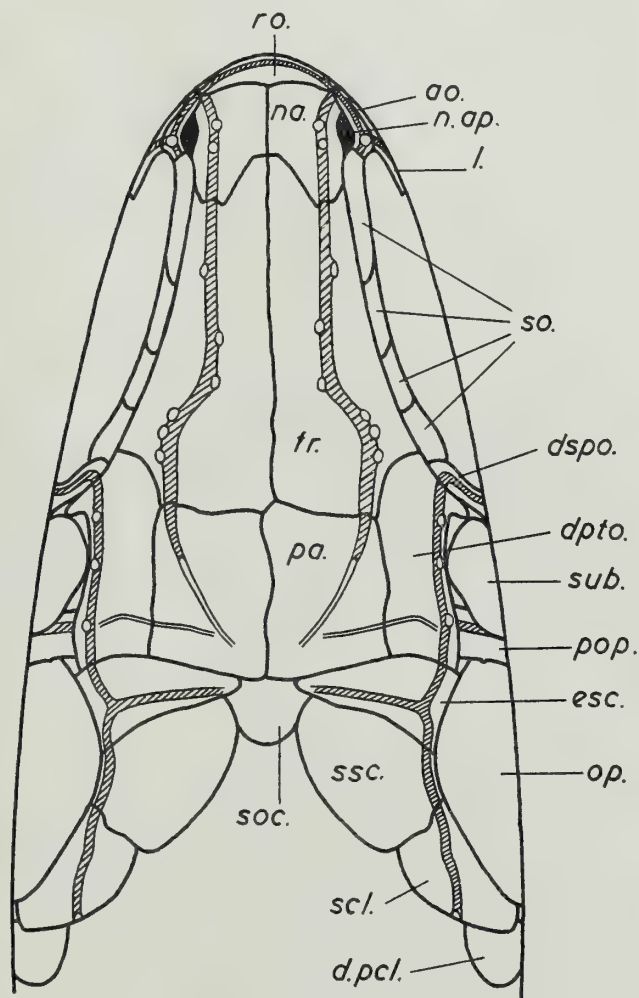


FIG. 1. *Ichthyokentema purbeckensis*. Reconstruction of skull and pectoral girdle in dorsal view. For explanation of lettering see p. 43.

supraorbitals. The frontal is ornamented with weak ridges which radiate from its centre, and are shorter and more irregular on the posterior part of the bone. Anteriorly, the frontal tapers and ends over the ethmoid.

The dermopterotic (dpto.) is a stout, rectangular bone which forms the roof of the post-temporal fossa, meeting the parietal medially and the autopterotic ventro-laterally. At the posterior edge of the orbit the dermopterotic bears a process pointing ventro-laterally: the dermosphenotic articulates with the anterior face of this process, and its posterior face forms the anterior wall of the dilatator fossa. The dermopterotic is ornamented with short, irregular ridges radiating from the middle of its lateral edge. The main cephalic sensory canal entered the dermopterotic from the extrascapular through a large pore in the posterior edge of the bone, above the lateral part of the post-temporal fossa. The preopercular sensory canal passed ventrally to the preopercular through a large pore at the posterior end of the lateral edge of the dermopterotic. Passing forwards through the dermopterotic, the canal

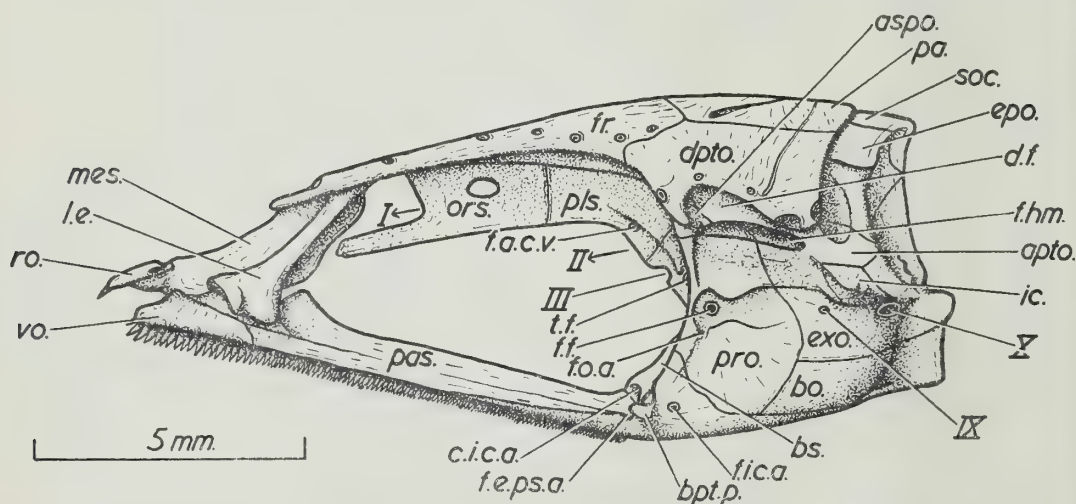


FIG. 2. *Ichthyokentema purbeckensis*. Reconstruction of neurocranium in lateral view. For explanation of lettering see p. 43.

gave off two branches through pores in the dorso-lateral edge of the bone, and then passed into the dermosphenotic through a pore in the anterior edge of the postorbital process. The supraorbital sensory canal did not anastomose with the infraorbital sensory canal. In some specimens the supraorbital canal ends posteriorly at the posterior edge of the frontal, but in most specimens it passes into the parietal and may extend for half the length of this bone (P. 44923). In the frontal, the supra-orbital canal ran from end to end of the bone in a tube which roughly follows the contour of the edge of the bone. The canal gave off between five and seven branches through pores in the frontal. The number and position of these pores varies from specimen to specimen, and from side to side of the same specimen, but there is usually a cluster of three pores above the posterior edge of the orbit. The canal passed forwards to the nasal from the anterior end of the frontal. The anterior pit-line runs back postero-medially across the parietal from the terminal pore of the supraorbital canal almost to the posterior edge of the bone. The middle pit-line runs transversely

from the region of the hind end of the anterior pit-line, and extends almost to the lateral edge of the dermopterotic, where it ends over the main cephalic canal.

The nasal (na., Pl. 2, fig. 5) (P. 8379 ; P. 7640 ; P. 44924-25) is a roughly triangular bone which carried the terminal part of the supraorbital sensory canal in a tube near its lateral edge. The nasals met in the mid-line through the greater part of their length. A shallow notch in the lateral edge of each nasal formed the dorsal margin of a narial aperture (n.ap.) : both nostrils may have opened through this single aperture, but it is possible that there was an anterior nostril between the antero-lateral edge of the nasal, the rostral and the antorbital. The pointed posterior end of the nasal articulated with the frontal, and received the sensory canal from the latter. The sensory canal gave off two branches through pores in the nasal, and passed forwards from the anterior end of the bone to anastomose with the ethmoid commissure at the junction between the antorbital and the rostral. Medial to the tube which contained the sensory canal the nasal bears a few ornamental bosses.

The ethmoid region is well ossified superficially, but in life the bone was a thin sheet over the surface of a block of cartilage which was exposed ventrally. There is no visible suture separating the mesethmoid and lateral ethmoid. The mesethmoid (mes.) is represented by a median ridge running forwards beyond the frontals, and widening anteriorly where the rostral articulates with its dorsal surface. The lateral ethmoid (l.e.) is represented by a strong wing extending antero-ventrally beneath the frontal. The lachrymal articulated with the thickened ventro-lateral edge of this wing, and the palatine articulated with the cartilage capping the ventral edge of the wing. Between the mesethmoid and lateral ethmoid regions there is a large depression, open dorsally, which housed the olfactory organ.

The rostral (ro., Pl. 2, figs. 4, 5) (P. 8379 ; P. 44926-27) is a median, triangular bone overlying the tip of the mesethmoid and projecting beyond the latter. The anterior edge of the bone bears a single row of about a dozen small teeth. There is a projection on the lateral edge of the bone with which the premaxilla articulated. The rostral commissure, received laterally from the antorbital, ran in a closed tube across the posterior part of the bone.

The vomer (vo.) (P. 44927-28) is thick and broad, and bears about 50 stout, slightly curved teeth on its ventral face. On the dorsal surface of the bone there is a pair of short wings which meet the mesethmoid above. The head of the maxilla articulated with a facet at the base of the wing of the vomer, and the palatine articulated with the lateral edge of the bone. The vomer is a median bone and shows no sign of a paired origin : it thus resembles the vomer of teleosts. The vomer is not known in any other halecostome, nor is it known in parasemionotids.

The parasphenoid (pas.) (P. 44927 ; P. 44929-30) is long and stout. It is narrow below the orbit, but widens anteriorly, where it ends in a groove on the dorsal surface of the vomer. The parasphenoid bears an elongated patch of teeth which extends from its anterior end to the level of the basipterygoid process. The teeth grow smaller posteriorly as the patch of teeth narrows. Below the orbit the bone bears a median crest which gave insertion to the ventral edge of the membranous interorbital septum. This crest ends posteriorly at the level of the pedicel of the

basisphenoid, which articulated with its hind edge. Behind this crest there is in some specimens (e.g. P. 44931-32) a wide bucco-hypophysial canal (b.h.c.) which passes obliquely antero-ventrally through the bone, but this canal is not a constant feature. An open bucco-hypophysial canal is a primitive feature which has so far

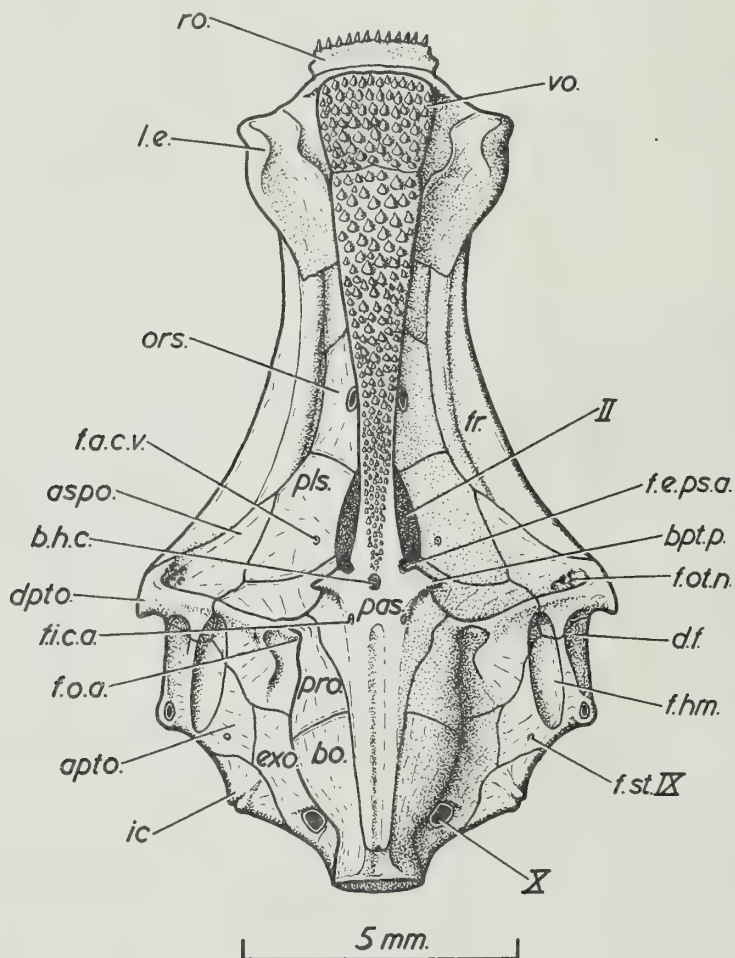


FIG. 3. *Ichthyokentema purbeckensis*. Reconstruction of neurocranium in ventral view.
For explanation of lettering see p. 43.

been observed among actinopterygians only in a few chondrosteans and in the teleost *Elops* (Olsson, 1958).

At the hind edge of the orbit the parasphenoid bears a short basipterygoid process (bpt.p.) which is shorter than those of both *Leptolepis* and *Pholidophorus*. The ascending process of the parasphenoid, behind the basipterygoid process, is short and delicate. The foramen of the internal carotid artery (f.i.c.a.) lies in the centre

of the ascending process. A notch (f.e.ps.a.) at the base of the anterior edge of the basiptyergoid process marks the passage of the efferent pseudobranchial artery (in some specimens, e.g. left side of P. 44933, this notch is enclosed within the bone as a foramen). The posterior part of the parasphenoid meets the prootic and basioccipital: it closes the myodome ventrally and ends just in front of the occipital condyle.

On the internal face of the ascending process of the parasphenoid, antero-dorsal to the internal carotid foramen, there is a bar of bone passing medially to meet the tip of the basisphenoid (Text-fig. 5; P. 44930-33): the internal carotid and the palatine nerve passed forwards below this bar.

The basioccipital (bo.) (P. 44927; P. 44934-35) forms the major part of the occipital condyle. The notochord pit, in the centre of the basioccipital condyle, is very long, and extends to the anterior edge of the basioccipital. This is a primitive feature recalling the chondrosteans. The anterior part of the basioccipital consists of a lateral wall which bulges out to meet the prootic anteriorly and the exoccipital above, and a broad median crest which tapers anteriorly and meets the similar crest formed by the prootics. The lateral wall forms the wall of the otolith chamber while the median crest separates the otolith chambers and encloses the notochord pit. On the ventral surface of the basioccipital there is a median groove which is bridged by the parasphenoid, but there is no groove or canal for the dorsal aorta as there is in *Pholidophorus bechei* (Rayner, 1948: 322) and *Leptolepis coryphaenoides* (Rayner, 1937: 57).

Each exoccipital (exo.) forms a small triangular exoccipital condyle applied to the dorso-lateral edge of the basioccipital condyle. The triangular foramen magnum (f.m.) is enclosed between the exoccipitals above the occipital condyle. Lateral to the foramen magnum, the exoccipital bears several small, projecting crests (Text-fig. 4). These crests may mark the insertion of the anterior myocommata on the skull, or they may be the sites of insertion of ligaments binding the first neural arch to the skull. The occipital nerves emerged through one or two small foramina between the crests on the exoccipital (f.o.n.) (P. 44936-37). On the posterior face of the neurocranium the exoccipital touches the supraoccipital dorsally, and meets the epiotic dorso-laterally and the autopterotic laterally, the suture with the latter being partially overlain by the intercalar. On the lateral face of the neurocranium the exoccipital meets the prootic and basioccipital, forming with these bones the wall of the otolith chamber, and meets the autopterotic above, though the suture with the latter bone is never clear, and the bones were evidently more or less fused. The large vagus foramen (X) opens postero-laterally at the posterior edge of the lateral face of the exoccipital. The glossopharyngeal foramen (IX) lies near the anterior edge of the lateral face of the bone. Internally, the exoccipitals form the posterior part of the floor of the cranial cavity, where they overlie the median crest of the basioccipital and form the posterior margin of the fenestra between the otolith chamber and the cranial cavity (P. 44934).

The autopterotic (apto.) forms the floor of the posterior part of the post-temporal fossa, and meets the autosphenotic anteriorly, the epiotic medially, the exoccipital postero-ventrally and the prootic antero-ventrally. Laterally the autopterotic

meets the dermopterotic, which roofs the post-temporal fossa. The autopterotic appears to be fused with the dermopterotic anteriorly, above the dilatator fossa. In the anterior part of the floor of the post-temporal fossa there was an area of cartilage (c.t.f., Pl. 3, fig. 8) which separated the autopterotic from the autosphenotic. The posterior three-quarters of the elongated facet for the hyomandibular (f.hm.) is borne on the ventral face of the autopterotic, and above this facet the shallow posterior part of the dilatator fossa (d.f.) is excavated in the lateral edge of the bone. Medial to the hind end of the hyomandibular facet, the autopterotic is perforated by a small foramen (f.st.IX) which transmitted the supratemporal branch of the glossopharyngeal nerve upwards across the post-temporal fossa to the sensory canal on the skull roof (P. 44934). Internally, the autopterotic enclosed the external

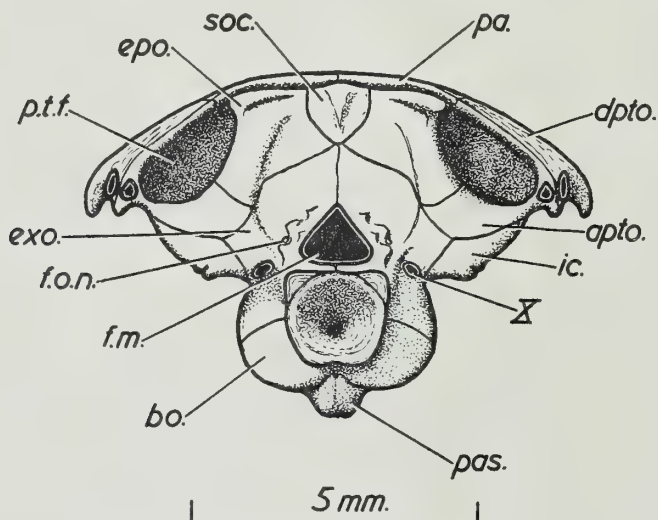


FIG. 4. *Ichthyokentema purbeckensis*. Reconstruction of neurocranium in posterior view. For explanation of lettering see p. 43.

semicircular canal and the ventral part of the posterior semicircular canal (P. 44934). The intercalar (ic.) (P. 44938) is the usual small, superficial bone, plastered on the surface of the exoccipital and autopterotic. Two knobs with a notch between them mark the insertion on the bone of the ligament from the ventral limb of the suprascapular.

The epiotic (epo.) forms the postero-dorsal shoulder of the neurocranium, as usual. The anterior part of its dorsal surface is overlain by the parietal and dermopterotic, and the extrascapular and suprascapular articulated with its exposed dorsal surface. Laterally, the epiotic forms the medial wall of the post-temporal fossa, meeting the autopterotic below. The epiotics are separated by the supraoccipital, and they meet the exoccipitals on the posterior face of the neurocranium. The angle between the lateral and posterior faces of the epiotic forms a thickened buttress within which the dorsal part of the posterior semicircular canal was enclosed (p.s.c., Pl. 3, fig. 8) (P. 44934.)

The supraoccipital (soc.) is moderately large, being overlain by the parietals anteriorly, and extending down the posterior face of the neurocranium to touch the exoccipitals. There is a small, knob-like crest on the posterior face of the bone. It is possible that the supraoccipital was exposed on the skull roof between the medial edges of the extra- and supra-scapulars, but this is not certain.

The autosphenotic (aspo.) is a rather small bone, underlying the frontal and dermopterotic, and meeting the prootic below and autopterotic behind. Anteriorly the bone tapers to a point between the frontal and the pleurosphenoid. The broad upper part of the ridge marking the hind edge of the orbit is formed by the autosphenotic, and behind this ridge the bone forms the antero-dorsal corner of the hyomandibular facet. Above the hyomandibular facet the autosphenotic bears the anterior part of the dilatator fossa (d.f.), an excavation which housed the dilatator muscle of the operculum. In the dorso-lateral corner of the orbit there are several small pits (f.ot.n.) in the autophenotic which mark the passage of the otic branch of the facial nerve.

The post-temporal fossa (p.t.f., Text-fig. 4) is completely roofed by the dermopterotic. The fossa has a large, oval posterior opening, and extends forwards, tapering as it does so, as far as the hind edge of the orbit (P. 44934), where it ends between the autosphenotic and dermopterotic.

The prootic (pro.) (P. 44934 ; P. 44939-40), as usual, is the most complex bone in the neurocranium. The ventral part of the bone consists of an outer lamella which bulges out to form the anterior part of the wall of the otolith chamber, and an inner lamella which separates the myodome from the otolith chamber and meets its fellow above the myodome in the prootic bridge (pro.b., Text-fig. 5 ; Pl. 3, fig. 8). The inner and outer lamellae meet anteriorly in the posterior edge of the orbit. The dorsal part of the prootic consists of a lateral region which meets the autosphenotic and the autopterotic, and forms the antero-ventral corner of the hyomandibular facet, and an anterior region which forms the posterior wall of the orbit, meeting the pleurosphenoid above and being separated from its fellow by the wide median optic fenestra (II). Between the dorsal and ventral parts of the bone, lateral to the prootic bridge, the prootic contains the trigemino-facialis chamber. The chamber is divided by a wall of bone into an internal pars ganglionaris and an external pars jugularis, as it is in teleosts, *Leptolepis*, *Pholidophorus* and most fossil holosteans. The pars ganglionaris is a very shallow recess on the medial face of the prootic. The geniculate ganglion certainly lay within the pars ganglionaris, since the palatine nerve left the main trunk of the facial before the latter emerged from the facial foramen. The position of the Gasserian ganglion is not certain : it may have lain in the pars ganglionaris or it may have lain partially or completely outside the prootic, on the orbital surface of the bone. The pars jugularis is a longitudinal groove on the lateral face of the prootic. The lateral wall of the pars jugularis is very poorly ossified ; in some specimens (e.g. P. 44941-42 ; Text-figs. 2, 3, 5) there is a narrow bar of bone bridging the anterior end of the groove, but in others (e.g. P. 44934-39) there are two processes in this region which fail to meet each other. The ridge marking the upper edge of the pars jugularis is stronger than that marking the lower edge, and can be traced back on to the exoccipital.

The jugular vein ran in this groove, passing back from the orbit below the lateral wall of the groove where the latter is present. The course of the orbital artery, passing up from the internal carotid, is marked by a break in the ventral edge of the jugular groove (f.o.a., Text-figs. 2, 3) above the internal carotid foramen. The orbital artery passed forwards into the orbit with the jugular vein. Only one foramen leads from the pars ganglionaris into the pars jugularis: this is the facial foramen (f.f., Text-figs. 2, 5; Pl. 3, fig. 8) which, in about half the specimens, transmitted only the hyomandibular trunk of the facial nerve. Within the bone, there are two canals leaving the floor of the facial foramen. The larger of these passes antero-ventrally into the dorso-lateral corner of the myodome, and transmitted the palatine

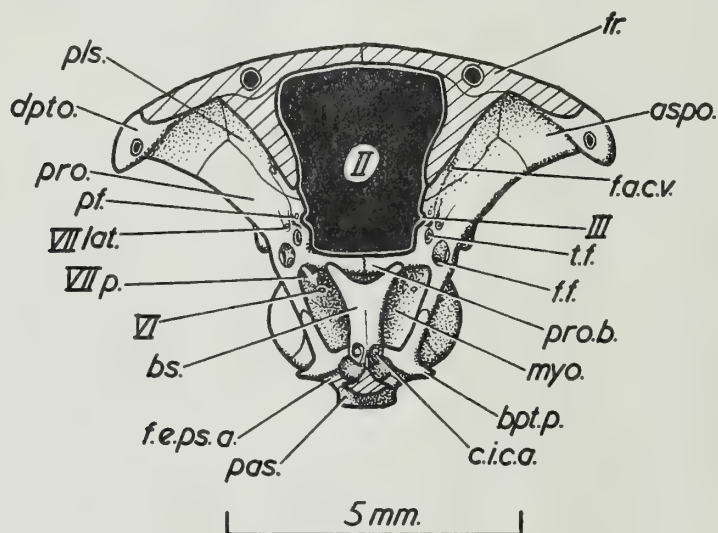


FIG. 5. *Ichthyokentema purbeckensis*. The reconstructed neurocranium cut through immediately anterior to the basisphenoid and viewed from the front. For explanation of lettering see p. 43.

nerve (VII p., Text-fig. 5). The smaller canal passes postero-ventrally through the prootic in front of the otolith chamber. Though this second canal is a constant feature, it could not be traced to an external opening in any specimen, and it may have carried a blood vessel. The trigeminal foramen (t.f., Text-figs. 2, 3, 5; Pl. 3, fig. 8) opens on the orbital face of the prootic, and the trigeminal nerve did not enter the pars jugularis. On the medial face of the prootic, in the pars ganglionaris, the trigeminal foramen lies antero-dorsal to the facial foramen. In about half the specimens in which this region is visible there is a third foramen which lies immediately above the facial foramen (P. 44939) or is confluent with the latter (P. 44943-44; right side of P. 44940), and which opens on the orbital surface of the prootic just postero-dorsal to the trigeminal foramen (VII lat., Text-fig. 5). This foramen must have transmitted the lateralis branches of the facial nerve, the buccal, otic and superficial ophthalmic nerves. In other specimens (P. 44933-34; P. 44941;

left side of P. 44940) this foramen is absent, and the lateralis branches of the facial nerve passed through the facial foramen and forwards into the orbit with the jugular vein. In the orbital edge of the prootic, anterior to the trigeminal foramen, there is a notch (III) which marks the passage of the oculomotor nerve. Between the trigeminal foramen and the oculomotor notch there is a knob from which a ridge passes dorsally, widening as it does so. The superficial ophthalmic nerves and the otic nerve passed upwards behind this ridge. In some specimens the knob in front of the trigeminal foramen is perforated by a small canal (pf., Text-fig. 5) (P. 44943-44) leading forwards towards the oculomotor notch; this small canal must have transmitted the profundus nerve, and indicates that this nerve normally emerged through the trigeminal foramen. In P. 44940 there is a separate foramen for the profundus nerve in front of the trigeminal foramen. The abducens nerve passed ventrally into the myodome through a small foramen (VI, Text-fig. 5; Pl. 3, fig. 8) in the prootic bridge. Behind the internal openings of the trigeminal and facial foramina there is a large recess on the internal face of the prootic which housed the ampullae of the anterior and external semicircular canals, and the anterior part of these canals was enclosed within the prootic lateral to this chamber (a.s.c., Pl. 3, fig. 8) (P. 44934).

The mydome (myo., Text-fig. 5) is wide at its orbital opening, but tapers rapidly and ends at the posterior edge of the prootic, without entering the basioccipital. The floor of the myodome is formed by the parasphenoid. The myodome does not open posteriorly.

The otolith chamber is large, with a rather strongly inflated lateral wall (Text-figs. 3, 4, 5), and extends to the ventral edge of the prootic and basioccipital, though it is closed ventrally by these bones and not by the parasphenoid. The chamber communicates with the cranial cavity above through a very large oval fenestra (f.o.c., Pl. 3, fig. 8).

The basisphenoid (bs., Text-figs. 2, 5) (P. 44930-33) has a short, stout pedicel which is inserted ventrally on the hind edge of the median crest on the parasphenoid, and a pair of short, slender arms which meet the edge of the prootic bridge, enclosing the pituitary fossa between them. The pedicel of the basisphenoid contains a pair of canals (c.i.c.a., Text-fig. 5) which transmitted the internal carotids upwards, and the arteries probably entered the cranial cavity through the wide optic fenestra (II, Text-fig. 5).

The pleurospenoid (pls.) (P. 44940-45) is a moderately large plate of bone which meets the frontal and autosphenotic dorsally, the orbitosphenoid anteriorly and the prootic behind, and is separated from its fellow by the optic fenestra. The posterior part of the bone bears a low ridge which is continuous with the ridge on the orbital face of the prootic. Below this ridge the bone contains a foramen (f.a.c.v., Text-figs. 2, 3, 5) which probably transmitted the anterior cerebral vein. The trochlear nerve probably passed through the optic fenestra.

The orbitosphenoid (ors.) (P. 44946-47) is a large median bone, "V"-shaped in section, meeting the frontal above and the pleurospenoid behind. The anterior margin of the optic fenestra is formed by a notch in the posterior edge of the bone. The antero-ventral edge of the bone bears a long median process which extended

forwards almost as far as the hind edge of the lateral ethmoid. The olfactory nerves emerged through a large foramen (I) above the base of this process, and ran forwards along the dorsal edge of the process. In the centre of the lateral face of the orbito-sphenoid there is a large oval fenestra (Text-figs. 2, 3; P. 44948).

(c) *Cheek and Upper Jaw*

In most of the more or less complete specimens the bones of this region are badly crushed. The fragmentary material from Lulworth, on the other hand, contains

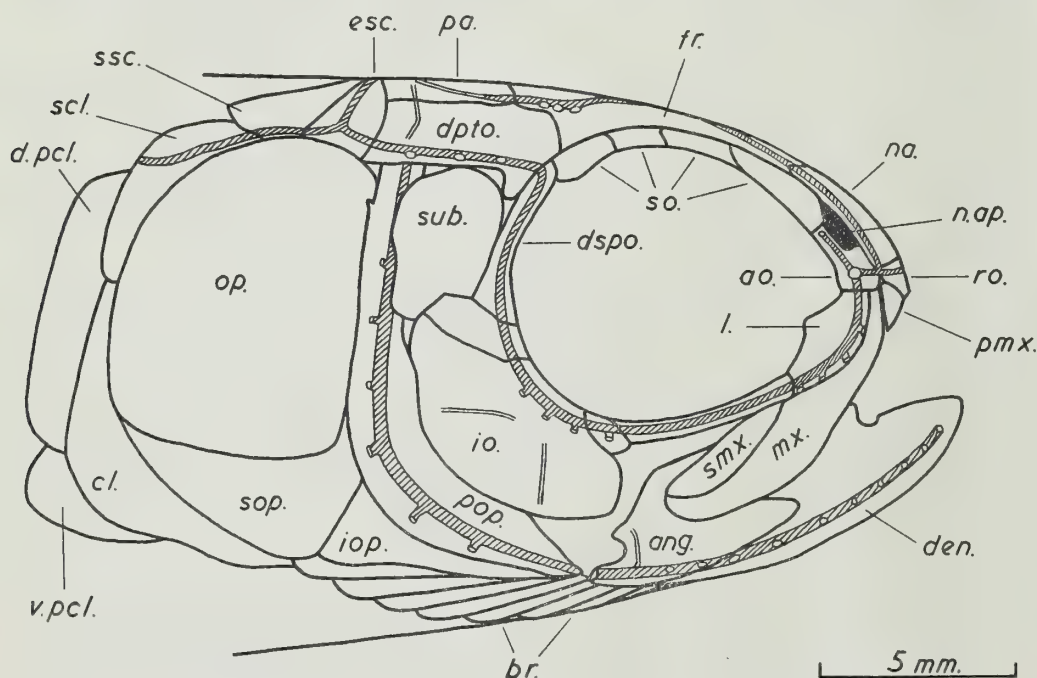


FIG. 6. *Ichthyokentema purbeckensis*. Reconstruction of skull and pectoral girdle in lateral view. For explanation of lettering see p. 43.

many fine examples of individual bones but these are detached from one another and from the neurocranium. Fortunately we were able to prepare one of the more complete specimens (P. 1073) to show the inner surfaces of some of the cheek bones (Pl. I, fig. 2), and, using mainly this specimen and the isolated bones from Lulworth, it has been possible to make a fairly accurate reconstruction of this part of the skull (Text-fig. 6).

The opercular series consists of the opercular, subopercular, interopercular and the branchiostegal rays. The opercular (op.) is a large bone, roughly one and a half times as high as it is long. Its strongly curved dorsal and posterior border overlaps the dermal bones of the pectoral girdle, the nearly straight ventral border overlies the dorsal part of the subopercular, and the sinuous, thickened, anterior border is

in turn covered by the preopercular. The ventral edge of the opercular lies approximately at right angles to the anterior edge. The articular facet for the hyomandibular lies near the anterior margin and roughly one-third of the distance from the dorsal to the ventral edge ; in some specimens its position is indicated by a small, rounded projection of the anterior margin. The external surface of the bone bears faint, concentric growth lines but is otherwise smooth.

The subopercular (sop.) is considerably smaller than the opercular. The part of the bone exposed on the surface of the skull was roughly triangular ; the anterior part of the dorsal margin is produced into a long, tapering, vertical process, nearly equal in height to the remainder of the bone, but this was completely concealed beneath the opercular and preopercular.

The interopercular (iop.) is a long, triangular bone lying in front of the subopercular and overlain dorsally by the preopercular. In P. 7640 the remains of five slender branchiostegal rays (br.) can be seen lying ventral to the interopercular. A broad median gular plate (g.p., Text-fig. 7) is present in P. 40635.

The preopercular (pop.) is long and curved. The ventral part of the bone is slightly expanded and strongly curved, with its lower end directed forwards. The dorsal part is narrower, straighter, and nearly vertical in position ; its upper end abuts against the dermopterotic. The curved postero-ventral border overlies the bones of the opercular series, the antero-dorsal edge is partly covered by the suborbital and the second infraorbital. The preopercular sensory canal ran through the bone giving rise to a number of short lateral branches along its posterior and ventral edges, and then continued on to the mandible.

The dermal bones surrounding the orbit are : the supraorbitals, the dermosphenotic, the infraorbitals, the lachrymal and the antorbital, which together form a complete ring around the orbit ; and the suborbital, which lies immediately behind the dermosphenotic. In P. 1073 a chain of four supraorbitals (so.) can be seen. The first is small, unusually thick, and in contact posteriorly with the dermosphenotic. The next two are thinner, the second is shorter than the first and the third longer. The fourth supraorbital is nearly as thick as the first and more than twice its length. It is in contact antero-dorsally with the frontal and nasal, antero-ventrally with the antorbital and its anterior edge contributes to the border of the nasal aperture. The first and second supraorbitals bear elongated tubercles of ganoine on their external surfaces ; the third and fourth are known only from the internal surface. The dermosphenotic (dsp.) is a slightly curved, almost cylindrical bone, lying vertically with its upper part in contact with the front edge of the dermopterotic. The main cephalic sensory canal entered a little distance below the upper end of the bone, bent through a right angle, and continued parallel to the long axis of the bone as the infraorbital canal. In P. 1073 there are four infraorbitals (io.). One of these, the second counting from the dermosphenotic, is considerably larger than the others and partly overlies the preopercular. On the external surface of the second infraorbital can be seen the horizontal and vertical pit-lines of the cheek. The presence of these pit-lines on the second infraorbital of an undetermined species of *Pholidophorus* from the Lias of Lyme Regis has been recorded by Westoll (1937 : 376). The fourth infraorbital is a long slender bone. The lachrymal (l.)

bears a small facet for articulation with the lateral ethmoid. On its external surface, postero-dorsal to the sensory canal, the lachrymal bears a curved row of five prominent spines (P. 44978-79); P. 44979 bears in addition three or four small raised tubercles. The infraorbitals and the lachrymal contained the infraorbital sensory canal which gave off several short branches directed away from the orbit; the second and third infraorbitals and the lachrymal bearing three or four, one, and four such branches respectively. The antorbital (ao.) is a small bone containing the junction of the infraorbital and ethmoid sensory canals, and a short branch which extends postero-dorsally parallel to the supraorbital canal and ends just within the bone in

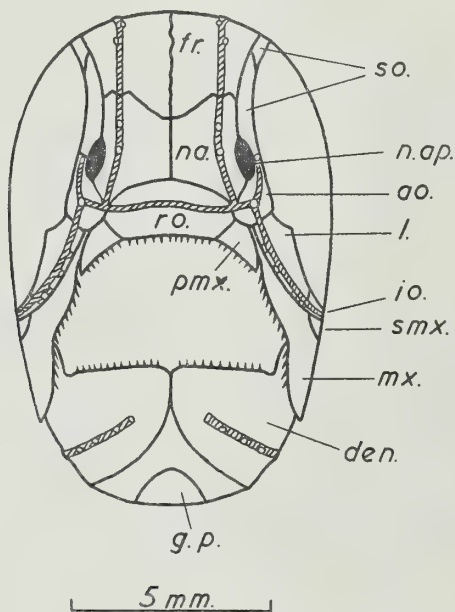


FIG. 7. *Ichthyokentema purbeckensis*. Reconstruction of the skull in anterior view. For explanation of lettering see p. 43.

a pore to the surface (P. 3607; P. 45020). A second pore opens directly into the junction of the three canals. The dorsal border of the antorbital bears a semicircular notch which forms the ventral edge of the narial opening. The bone is ornamented externally with two or three small spines. P. 1073 shows a single suborbital bone (sub.) of irregular shape lying immediately posterior to the dermosphenotic and first infraorbital.

Part of a bony sclerotic ring can be seen in P. 8378 and the material from Lulworth includes several isolated examples. As far as can be ascertained the sclerotic ring was a continuous structure and not divided into a number of separate ossifications.

The upper jaw contains the premaxilla, maxilla and one supramaxilla. The bones are shown in lateral view in Text-fig. 6.

The premaxilla (pmx., Pl. 2, fig. 5) (P. 8379 ; P. 44956) is a small, roughly triangular bone bearing about ten teeth in a single row along its oral border. The premaxillae did not meet in the mid-line, but were separated by the rostral. A small notch on the medial edge of the premaxilla articulated with a projection on the lateral edge of the rostral. A projecting facet in the centre of the dorsal edge of the premaxilla articulated with the antero-ventral corner of the antorbital.

The maxilla (mx.) (P. 1073 ; P. 44957) is rather short, and ends below the centre of the orbit. The bone bears a single row of teeth which extends along the entire length of its oral border. The rod-like head of the maxilla inclines medially at about 45 degrees to the body of the bone, and articulated with a facet at the base of the wing of the vomer. The premaxilla lay below and in front of the head of the maxilla. A slight thickening of the dorsal surface of the lateral part of the head of the maxilla marks the articulation of the maxillary process of the palatine. The maxilla is unornamented.

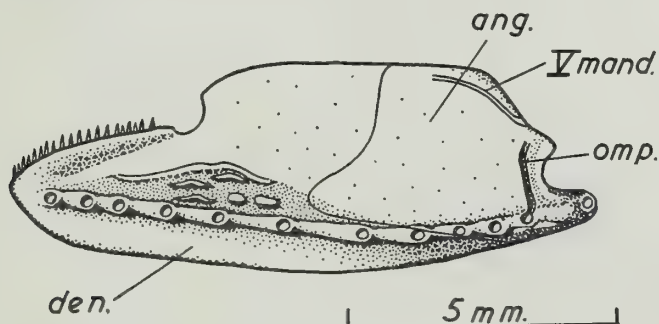


FIG. 8. *Ichthyokentema purbeckensis*. Reconstruction of left mandible in lateral view. Based mainly on P. 44973-75 and P. 45031. For explanation of lettering see p. 43.

The single supramaxilla (smx.) (P. 7807 ; P. 3607 ; P. 44958) is an elongated slip of bone, pointed anteriorly, whose curved ventral edge fits against the dorsal part of the posterior half of the maxilla.

(d) Mandible

The lower jaw is composed of four elements : the dentary and angular, which together form the entire external or labial surface of the mandible ; the Meckelian bone ; and a single small coronoid (Text-figs. 8, 9 ; Pl. 4, fig. 9).

The dentary (den.) is the largest of these four bones. It is gently curved in the vertical plane so that the inner surface is concave and the outer convex ; in addition the anterior part of the bone shows a strong curvature in the horizontal plane towards the mid-line. From the anterior end of the dentary the dorsal margin is thickened for slightly less than half its length and this region bears teeth. In P. 12515 and P. 7640 these teeth can be seen as simple, conical structures from 0.6 to 0.8 mm in height. In the isolated mandibles, P. 44973-75, though the teeth themselves are missing their attachments to the jaw can be seen ; there appear to have been between 20 and 30 teeth arranged two or three deep along the edge of bone. The dentigerous

part of the dorsal margin is separated from the moderately well developed coronoid process by a small, rounded notch. The anterior and ventral edges of the bone are both gently curved. Posteriorly the dentary is in contact with the angular and extends backwards for a considerable distance ventral to that bone. A little distance above the ventral margin of the dentary, and lying roughly parallel to it, is the tube which contained the mandibular sensory canal. The canal was enclosed in a rather thicker portion of the bone so that this region is raised slightly above the general level of the external surface of the mandible. The canal gave off about twelve branches through pores along its length. Dorsal to the canal a triangular area of the dentary bears a number of short ridges or elongate tubercles of bone. On the internal surface there is a low longitudinal ridge directly above which is a shallow depression. The ventral part of the Meckelian bone fits into this depression with its ventral edge abutting against the dorsal edge of the longitudinal ridge. The dentary is thickest in the tooth-bearing region of the dorsal margin and around

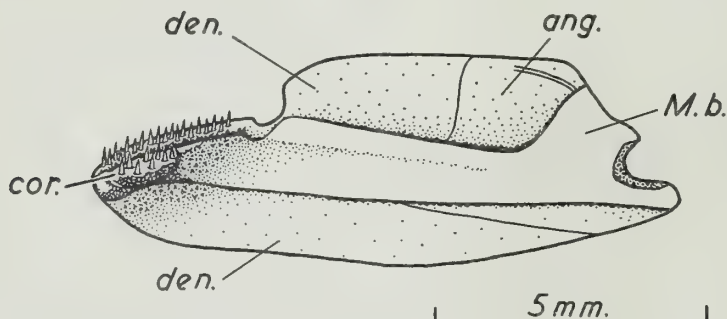


FIG. 9. *Ichthyokentema purbeckensis*. Reconstruction of right mandible in medial view. Based mainly on P. 44973-75. For explanation of lettering see p. 43.

and immediately dorsal to the sensory canal; thinnest on the coronoid process and near the ventral edge.

The angular (ang.) joins with the dentary in the formation of the coronoid process. The anterior and most of the ventral border of the bone is in contact with the dentary and the dorsal edge is continuous with that of the latter. The posterior border of the angular slopes backwards and downwards with a prominent semi-circular notch in the region of the jaw articulation. At the facet for the quadrate, although the angular and Meckelian bone are closely applied to each other, they are quite distinct, and the articular surface is formed by the Meckelian bone alone. In view of this the bone under discussion must be considered a true angular and is not an angulo-articular such as Rayner (1937: 53) has described in *Leptolepis coryphaenoides*. The mandibular sensory canal entered the angular near its posterior end and ran forward into the dentary. On the whole the canal lay deeper in the bone than in the dentary so that the enclosing bone projects less above the general surface. A little distance in front of the articulation the angular bears a short vertical pit-line—the oralo-mandibular pit-line (omp.)—which communicates at its lower end with the sensory canal. The postero-dorsal part of the bone encloses a

narrow, slightly curved canal (V mand.). Anteriorly the canal opens into a short groove on the external face of the angular, posteriorly by a foramen in the posterior edge of the bone a little distance above the jaw articulation. From its size and position it seems possible that this canal was traversed by a division of the mandibular branch of the fifth cranial nerve. On its internal surface the angular bears a continuation of the low, longitudinal ridge and shallow groove found on the dentary.

The Meckel's cartilage of the embryo has become ossified throughout its length to form a single continuous bone, without any sign of separate articular or mento-meckelian elements. This bone is referred to as the Meckelian bone (M.b.)—a term employed by Stensiö for the homologous structure in *Saurichthys ornatus* (Stensiö, 1925 : 107). The Meckelian bone is long and slender, and runs the whole length of the jaw. Posteriorly it is somewhat expanded, being developed into a coronoid process dorsally, and it forms the surface for articulation with the quadrate. In this region the bone is closely applied to the inner surface of the angular. Except for a small region near the extreme posterior end, the Meckelian bone lies with its ventral edge fitting into the shallow longitudinal depression in the angular and dentary and abutting against the longitudinal ridge which these bones bear. In the neighbourhood of the rounded notch in the dorsal edge of the dentary the Meckelian bone shows a similar notch or emargination in its dorsal edge. In front of this the bone tapers slightly, increases in thickness, and near and at the tip of the jaw becomes rolled upon itself so as to form an incomplete cylinder with unequally thickened walls and a small cavity which remains open on its medial side. Between the coronoid process and the rounded notch, the dorsal edge of the Meckelian bone is noticeably thicker than the very thin, more ventral portion. Apart from the contact between its ventral edge and the dentary and angular, the bone curves medially—away from the dermal bones. In the more anterior part of the jaw the bone lies close against the dentary and follows its curvature towards the median plane.

The single coronoid (cor.) is a small bone measuring only about 1.5 mm. in length, i.e. less than one-sixth of the length of the jaw. It lies in the anterior part of the jaw with its upper, tooth-bearing surface slightly below the level of the tooth-bearing region of the dentary. The dorsalmost part of its outer surface is in close contact with the inner surface of the thickened dorsal edge of the dentary ; the remainder of its outer surface fits into a shallow depression in the Meckelian bone. The coronoid bore about a dozen teeth. Two of the coronoid teeth can be seen in P. 44973 ; they are similar in structure and size to the teeth on the dentary.

(e) *Palate*

The palate is shown in medial view in Text-fig. 10. The hyomandibular (hm.) (P. 44950–51) is very broad, and lies almost vertically. The head of the bone is much broader than the facet on the neurocranium with which it articulates, and it must have been capped in life by a rounded mass of cartilage. The stout opercular process (op.p.) lies in the upper third of the bone. The ventral end of the bone is also broad, and this was capped by a mass of cartilage with which the interhyal

articulated. On the upper part of the anterior edge of the hyomandibular there is a short process which inclines antero-ventrally towards a process on the metapterygoid. The hyomandibular trunk of the facial nerve entered a large foramen (VII hm.) near the anterior edge of the bone at the level of the opercular process, and passed ventrally in a groove on the lateral face of the bone. This groove is bounded anteriorly by a vertical ridge against which the anterior edge of the preopercular lay.

The symplectic (sym.) (P. 8379) is a rod of bone which tapers distally and is inserted in a groove on the medial face of the quadrate. The symplectic inclines forwards at about 45 degrees to the hyomandibular.

The quadrate (q.) (P. 44952-53) is the usual triangular bone, bearing a double

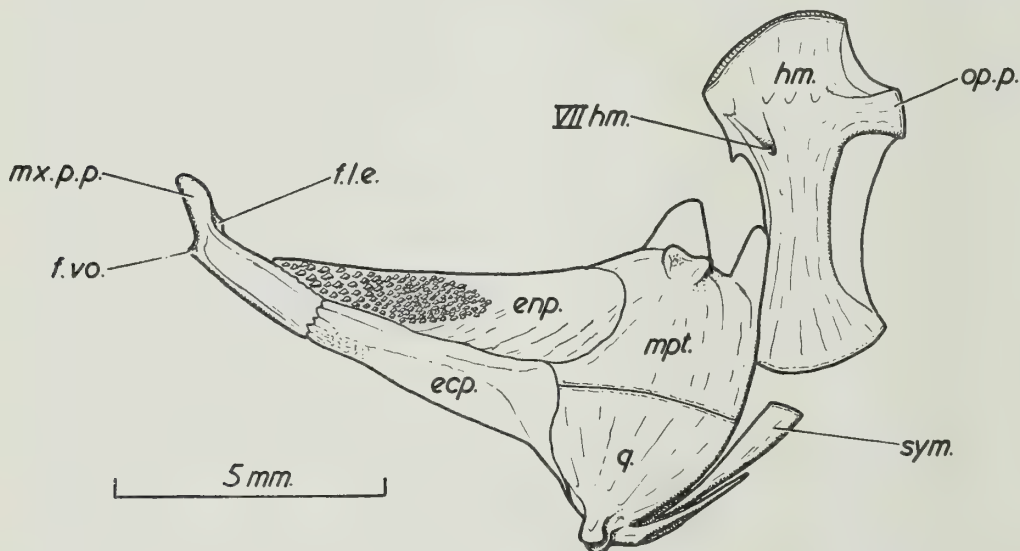


FIG. 10. *Ichthyokentema purbeckensis*. Reconstruction of palate of right side in medial view. For explanation of lettering see p. 43.

condyle for the articular. This condyle lay below the posterior half of the orbit. The quadrate bears a posterior process which forms the hind edge of the groove lodging the symplectic. The anterior edge of the preopercular lay against the posterior edge of this process, and the retro-articular process of the mandible abutted against a thickening at the base of the process.

The metapterygoid (mpt.) (P. 44953-54) consists of a broad plate of thick cancellous bone bearing two processes and a condyle on its dorsal edge. The ventral edge of the bone met the quadrate in a close suture, with no intervening cartilage. The condyle projects medially, and articulated with the basiptyergoid process of the parasphenoid. The anterior of the two processes is broad and delicate, and projects dorsally towards the short process on the anterior edge of the hyomandibular. The posterior process is strongly ossified, and projects dorso-laterally to meet the antero-lateral edge of the hyomandibular. The exact size of the anterior part of

the body of the metapterygoid is not yet known, and it is uncertain if there was a fenestra between it and the hind edge of the ectopterygoid.

The endopterygoid (enp.) (P. 8378 ; P. 44955) is an elongated strip of bone which tapers anteriorly. The dorsal edge of the bone inclines medially, and met the edge of the parasphenoid. The ventral edge of the bone fits against the dorsal edges of the palatine and ectopterygoid, and the posterior part of the bone lies against the medial face of the metapterygoid. The anterior half of the endopterygoid is covered with teeth. These curve forwards a little, and grow smaller posteriorly, as they do on the parasphenoid.

The ectopterygoid (ecp.) (P. 44956-57) is bent through about 45 degrees. Its tapering posterior limb meets the anterior edge of the quadrate and its long, stout anterior limb meets the palatine. At the postero-dorsal corner of the anterior limb of the bone there is a flange which lies medial to the quadrate and metapterygoid. The ectopterygoid bears no teeth, but the antero-ventral corner of the medial face of the bone is roughened.

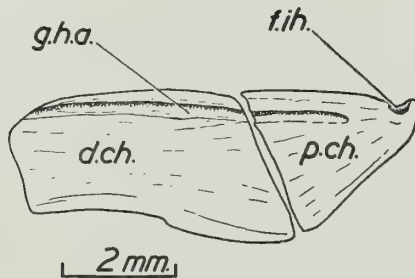


FIG. 11. *Ichthyokentema purbeckensis*. Reconstruction of left ceratohyal in lateral view.
For explanation of lettering see p. 43.

The palatine (P. 7640 ; P. 44958-59) is a small, elongated bone bearing a stout maxillary process (mx.p.p.) anteriorly. The maxillary process articulated with the dorsal surface of the proximal part of the maxilla. Saint-Seine (1949 : 301) speaks of a maxillary process on the palatine as being characteristic of the teleostean family Chirocentridae, and states that the presence of the process in *Thrissops* is an advanced character which foreshadows the chirocentrids. In fact, a maxillary process occurs on the palatine of almost all teleosts, and is not particularly characteristic of chirocentrids. The presence of a maxillary process in *Ichthyokentema* suggests that the process was probably present in most halecostomes. The palatines of *Pholidophorus* and *Leptolepis* are not well known, and the process may well have been present in them. The projecting antero-ventral edge of the palatine (f.vo.) articulated with the edge of the vomer, and a facet (f.l.e.) on the dorsal surface of the base of the maxillary process articulated with the cartilage capping the ventral edge of the lateral ethmoid. The palatine bears no teeth, but the bone appears to be entirely cartilagenous in origin, and it is possible that a toothed dermopalatine was loosely attached to its oral border.

(f) *Branchial Skeleton*

The skeleton of the hyoid and branchial arches is still very poorly known. The only part of the hyoid arch seen is the ceratohyal (Text-fig. 11; P. 44971-72). The ceratohyal is ossified in two pieces. The triangular proximal ossification (p.ch.) bears a facet (f.i.h.) for the interhyal at its postero-dorsal corner. The distal ossification (d.ch.) is rectangular, and is not perforated by a fenestra as it is in *Leptolepis* (Rayner, 1937 : 55). A groove (g.h.a.) for the afferent pseudobranchial artery crosses the lateral faces of both ossifications, and ends in front of the facet for the interhyal.

The branchial arches are known only by fragments, but the holotype shows that the first arch bore small teeth.

(g) *Axial Skeleton*

None of the material shows the vertebral column in its entirety. Three of the more complete specimens show a few vertebrae but the structure of the vertebrae can best be seen in some of the isolated specimens from Lulworth. The vertebral centra are thin cylinders of bone, almost invariably greater in diameter than in length (Text-fig. 12); out of approximately 90 vertebrae examined, in one only was the length of the centrum as great as its diameter. The anterior and posterior ends of the centrum are irregular and somewhat variable, though on the whole they tend to be arranged so that the length of the centrum is noticeably less dorsally than ventrally. Each neural arch (neu.) consists of a pair of structures attached at their lower ends to the dorsal or dorso-lateral surfaces of the centrum. The two halves of the neural arch are inclined backwards and meet each other a little distance above the centrum; they are quite firmly attached in this region though they can still be distinguished by the presence of superficial grooves and a change in the appearance of the bone. The region dorsal to the neural canal is preserved in only a small number of specimens. In some of these (P. 44976; P. 45021) the two halves of the neural arch appear to be continuous with a neural spine which is obviously of double origin but with the two halves firmly fused, in two other specimens (P. 45022-23) immediately dorsal to the neural arch lies an expanded portion of the bone with a hemispherical or cup-shaped socket which presumably served for the articulation of a neural spine. One of these specimens (P. 45023) appears to be from the caudal region, the other (P. 45022) may possibly be from the abdominal region; they may both have lain in the region of the dorsal fin. In the abdominal region each vertebral centrum bears a pair of short transverse processes (t.p.) arising from its ventro-lateral surfaces, each transverse process having an articulating surface for the head of the pleural rib (Text-fig. 12) (P. 45024). In the caudal region the transverse processes extend downwards and meet beneath the centrum to form the haemal arch. The two processes fuse and are then continued ventrally as a haemal spine, obviously of double origin, in a manner analogous to the neural spine born dorsally (P. 45021). It was impossible to ascertain the total number of vertebrae present in one individual.

Portions of seven or eight curved ribs can be seen in the anterior trunk region of

P. 8378, and fragments of similar ribs have been observed in the material from Lulworth; in P. 8378 they appear to have been about 5.5 mm. in length.

No traces of intermuscular bones have been found and it seems probable that none was present.

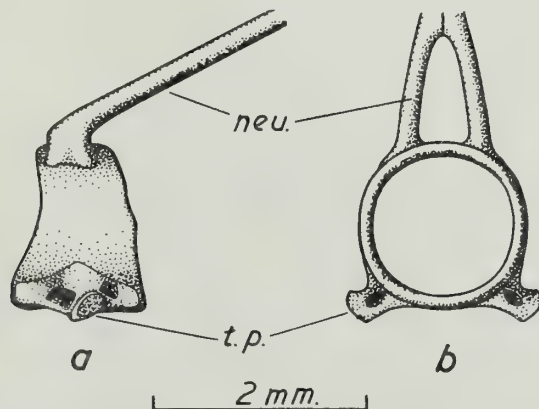


FIG. 12. *Ichthyokentema purbeckensis*. Reconstruction of trunk vertebra. *a*, in lateral view, *b*, in anterior view. Based mainly on P. 44976 and P. 45024. For explanation of lettering see p. 43.

(h) Appendicular Skeleton

The pectoral girdle is shown in lateral view in Text-fig. 6 and in medial view in Text-fig. 13.

The extrascapular (esc.) (P. 44963) is a triangular bone, tapering to a point medially. It is uncertain whether or not it met its fellow in the mid-line. The lateral line canal entered the postero-lateral corner of the bone from the suprascapular, and divided immediately within the bone into the main cephalic canal which passed forwards into the dermopterotic, and the supratemporal commissural canal which passed medially, giving off three or four branches through small pores en route.

The suprascapular (ssc.) (P. 44964) is large, and roughly equal in size to that of *Pholidophorus similis* (Saint-Seine, 1949 : 217). The bone may possibly have met its fellow in the mid-line, and its straight anterior edge fitted against the posterior edge of the extrascapular. The antero-lateral corner of the bone is thickened, and bears a slender process which passes antero-ventrally and was bound to the intercalary by ligaments. The lateral line canal, received from the supracleithrum behind, passed forwards to the extrascapular through a short canal at the extreme lateral edge of the bone. The surface of the suprascapular is ornamented with feeble ridges.

The supracleithrum (scl.) (P. 6171; P. 44965) is a blade-shaped bone with a thickened anterior edge. The head of the bone bears two projections which articulate with notches on the hind edge of the suprascapular. The lateral line canal, received posteriorly from the anterior lateral line scale, passed antero-dorsally through the

bone and emerged immediately below the lower of the two projections on the head of the bone. The surface of the supracleithrum is ornamented with feeble ridges.

The cleithrum (cl.) (P. 44966) is the usual large sigmoid bone. The anterior edge of the bone is thickened, and from the middle part of it a flange extends antero-

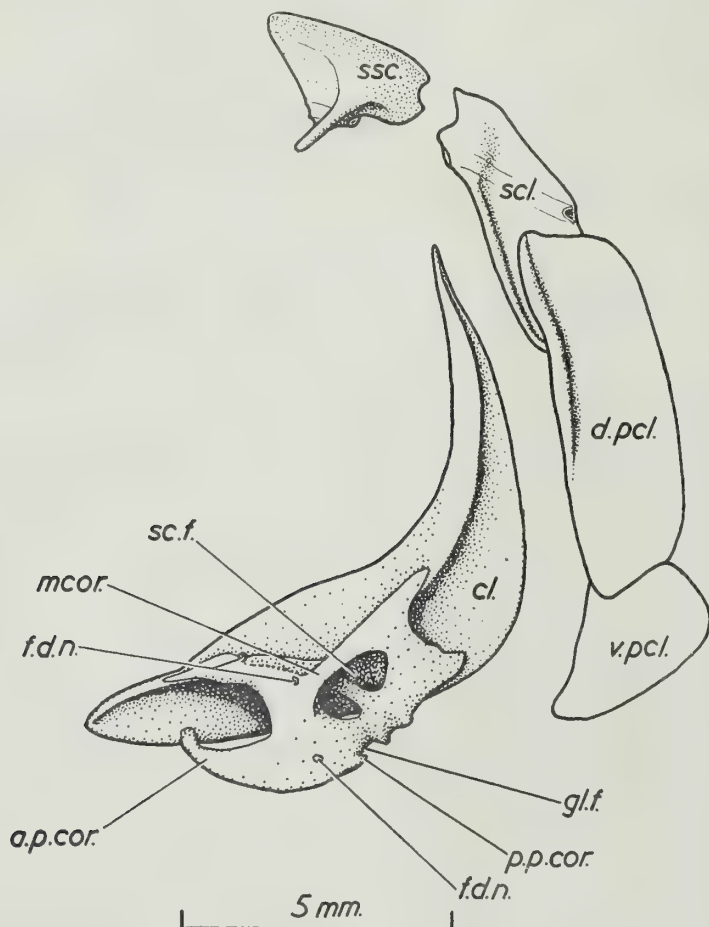


FIG. 13. *Ichthyokentema purbeckensis*. Reconstruction of pectoral girdle of right side in medial view. The supracleithrum and postcleithra are displaced posteriorly. For explanation of lettering see p. 43.

medially to form the hind edge of the opercular opening. Dorsally the bone tapers to a point which lay medial to the ventral end of the supracleithrum. The exposed lateral face of the cleithrum is ornamented with a few vertical ridges.

The endoskeletal pectoral girdle (Pl. 4, fig. 10) (P. 44966-68) is ossified in a single piece, with no sign of sutures between the scapular, coracoid and mesocoracoid elements. There is a very large scapular foramen (sc.f.) in the centre of the scapular region, and the foramen is divided horizontally by a strut of bone which passes

antero-laterally and attaches to the cleithrum. The glenoid facet (gl.f.) on the hind edge of the girdle inclines ventro-medially at about 45 degrees. The facet was covered in life by cartilage, and it is limited below by a very short posterior process of the coracoid (p.p.cor.). Above the glenoid facet the scapula bears a prominent saddle-shaped facet with which the anterior rays of the fin articulated, as in teleosts. A moderately stout mesocoracoid arch is present (mcor.), arching vertically over the medial face of the scapular foramen. The coracoid has a slender anterior process (a.p.cor.) which arches antero-ventrally and attaches to the lateral edge of the cleithrum some distance above the tip of the latter. The coracoid is pierced by three foramina (f.d.n.) which probably transmitted diazonal nerves, one lying at or near the junction of the bone with the cleithrum, one lying just in front of the base of the mesocoracoid arch and one lying near the posterior edge of the bone.

There are two postcleithra. The dorsal postcleithrum (d.pcl.) (P. 1073 ; P. 44969) is a large, rectangular bone lying medial to the supracleithrum and the dorsal part of the cleithrum and bearing a short flange which projects medially from its anterior edge. The ventral postcleithrum (v.pcl.) (P. 1073 ; P. 44670) is a trapezoid bone lying medial to the middle part of the cleithrum and the upper edge of the endoskeletal girdle. At the antero-dorsal edge of the bone there is a short pointed process which fits against the antero-ventral corner of the dorsal postcleithrum.

The radials of the pectoral fin are known only by very incomplete fragments, and their number is not known.

The pectoral fins are, at best, poorly preserved. They appear to have contained at least 11 rays, the first of which is stouter than the remainder. In specimen P. 8379 traces of fulcral scales can be seen lying along the anterior face of the first fin-ray. Some, at least, of the rays were jointed and may have branched.

The pelvic girdle is not known but the pelvic fins are on the whole slightly better preserved than the pectoral. They are a little smaller than the latter and contained more than five rays, the first of which bears five or six fulcral scales. All the rays are jointed and all except the first branch distally.

The dorsal fin is roughly triangular in shape and contained nine rays. All the rays are jointed and branched. The first fin-ray is bordered by six fulcral scales and these are preceded by two basal fulcra.

The endoskeleton of the anal fin can be seen in specimens P. 7640, P. 12515 and P. 8378. In P. 7640 six radials are exposed. The first of these lies opposite the base of the first fin-ray, the second lies close to the first and resembles it in length and stoutness, the remainder are rather more widely spaced and decrease gradually both in length and in thickness. In some specimens traces of the radials of the dorsal fin can be observed but these are not so well exposed as those of the anal fin just described.

The anal fin is approximately equal in size to the dorsal and closely resembles it in shape and construction. It contained seven rays in P. 8378 and six rays in P. 7640. As in the dorsal fin there are six fringing fulcra and two basal fulcra.

The caudal fin is bilobed and roughly symmetrical apart from the presence of a small scale-covered lobe of the body that extends dorsally for about one-third of the distance to the tip of the epicaudal lobe. Nothing can be seen of the endoskeleton

of the caudal fin. In P. 8378 the fin contains 19 principal rays, 17 of which are branched. The outermost ray of the upper lobe bears about ten fulcra, grading into the dorsal ridge scales anteriorly. The outermost ray of the lower lobe bears eight fulcra, and is preceded by three short, jointed, but unbranched rays, the last of which bears one fulcral scale.

(j) Squamation

The squamation has been described in detail by Smith Woodward (1919: 110) and, apart from details of the internal structure of the scales, little can be added to his account

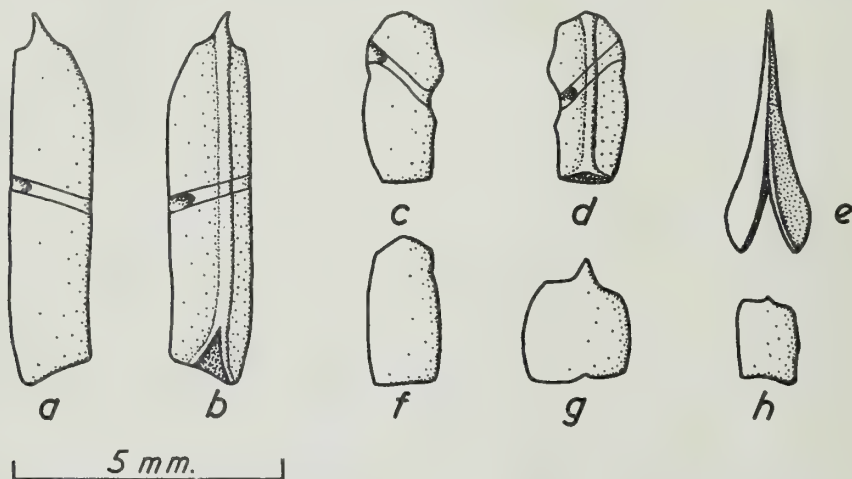


FIG. 14. *Ichthyokentema purbeckensis*. Unrestored drawings of scales: *a*, anterior scale of lateral line series in external view, from P. 45025; *b*, same scale in medial view; *c*, posterior scale of lateral line series in external view, from P. 45026; *d*, same scale in medial view; *e*, dorsal or ventral ridge scale from caudal peduncle, external surface, from P. 45027; *f*, scale from posterior trunk or anterior caudal region adjacent to lateral line series in lateral view, from P. 45028; *g*, scale from anterior trunk region towards dorsal or ventral mid-line, external surface, from P. 45029; *h*, scale from caudal region in lateral view, from P. 45030. In *a-d*, *f-h* dorsal is towards the top of the page; anterior is to the left in *a*, *c*, *f*, *g* and *h*; to the right in *b* and *d*; and towards the bottom of the page in *e*.

The scales are of moderate thickness, the external surfaces are smooth and the posterior edges without serrations. They are strengthened on their inner surfaces by a conspicuous vertical ridge (Text-fig. 14*b*, *d*). The scales of the trunk region articulate by a peg-like projection of the upper edge fitting into a V-shaped depression in the inner face of the lower part of the scale above (Text-fig. 14*a*, *b*, *g*). In the caudal region this articulation is considerably reduced in extent (Text-fig. 14*c*, *d*) or altogether absent. There appear to be nearly forty obliquely vertical rows of scales. In the anterior trunk region the scales of the lateral line series are very deep relative to their length, the ratio of scale height to length being as high as 4.1 to 1 in the region immediately behind the pectoral girdle. The relative height of the

scales decreases gradually as this series is traced back to the tail region and more rapidly along each of the obliquely vertical rows as one gets further from the lateral line. Near the dorsal and ventral surfaces in the trunk region, and in the caudal region the scales are approximately diamond-shaped (Text-fig. 14g, h). The caudal fin is preceded dorsally and ventrally by a small number of ridge scales (Text-fig. 14e), but these are not especially conspicuous. A few slightly enlarged, rounded scales lie in or near the mid-line a little distance anterior to the anal fin; in specimen P. 8378 one of these scales shows two denticulations posteriorly.

The scales are of the "lepidosteoid" type (Goodrich, 1908 : 758). Externally there is a well marked layer of enamel or ganoine which forms approximately one-tenth of the total thickness of the scale. The remainder of the scale consists of bone. This contains numerous, well developed and evenly distributed cell spaces and the canals of Williamson (Pl. 2, fig. 6). The latter are not particularly numerous and rather narrow; they end a little distance below the ganoine layer.

V. DISCUSSION

(a) *The systematic position of the genus Ichthyokentema*

In 1941 A. S. Woodward split the genus *Pholidophorus* Agassiz into four. Some species were retained within the genus, the remainder he distributed amongst three new genera—*Pholidophoroides*, *Pholidophoristion* and *Ichthyokentema*. Woodward's new genus *Ichthyokentema* contained only *I. purbeckensis* (Davies) and *I. brevis* (Davies); in our opinion *I. brevis* is a synonym of *I. purbeckensis* (see p. 7). In the case of *Ichthyokentema* Woodward justified the erection of a new genus on the grounds that in it the lateral line scales are relatively deeper, and the fulcra and the dorsal and anal fins are relatively larger than in his restricted genus *Pholidophorus*. Woodward's splitting of the genus *Pholidophorus* has not generally been accepted, and has been criticized by Saint-Seine (1949 : 29), rightly in our opinion, as being based on insufficient characters. However, the present description of *Ichthyokentema* shows that Woodward was correct in erecting this genus, though the characters which distinguish it from *Pholidophorus* are more numerous and of greater importance than those he mentioned. His other two genera—*Pholidophoroides* and *Pholidophoristion*, have not been investigated, and as the structure of the species allocated to them is only poorly known they will not enter into this discussion.

Of the many species of *Pholidophorus* known, only the Liassic *P. bechei* Agassiz (the type species) and the Kimeridgian *P. similis* A. S. Woodward, both included by Woodward in his restricted genus *Pholidophorus*, have been described in detail; the former by Rayner (1948 : 318) and the latter by Saint-Seine (1949 : 215). If correctly interpreted by these two authors, it seems unlikely that the two species can be congeneric, for, according to Saint-Seine, in *P. similis* the supraorbital sensory canal passed from the nasal into the rostral, and there was no connection between the dorsal branch of the infraorbital canal in the antorbital and the supra-orbital canal, while, according to Rayner, in *P. bechei* the supraorbital canal from the nasal connected with the dorsal branch in the antorbital, and the supraorbital

canal had no connection with the ethmoid commissure. Of these two arrangements, that in *P. similis* agrees with the conditions in the parasemionotids and in *Ichthyokentema*, and it seems possible that the structure of *P. bechei* has been misinterpreted. Assuming this to be so for the present discussion, *Ichthyokentema* differs from *Pholidophorus* as represented by *P. bechei* and *P. similis* in the following characters:

1. The presence of teeth on the rostral and the separation of the premaxillae by this bone.
2. The broad median contact between the nasals, with little or no separation of the nasals by the frontals.
3. The large number (four) of supraorbitals.
4. The presence of a toothed coronoid and a fully ossified Meckelian bone in the mandible (Rayner (1948 : 319) mentions a separate prearticular in *P. bechei*, but this bone bore no teeth, and may represent part of the Meckelian bone).
5. The presence of an oral pit-line on the mandible.
6. The presence of a strong dentition on the vomer, parasphenoid and endopterygoid.
7. The absence of an aortic groove or canal below the occipital region of the neurocranium.
8. The pedicel of the basisphenoid is stout and contains a pair of canals for the internal carotid artery.
9. The suture between the opercular and subopercular is almost horizontal in *Ichthyokentema*, but is strongly inclined in *Pholidophorus*.
10. The presence of two postcleithra (only one postcleithrum is known in *Pholidophorus*, but a second one was possibly present since it occurs in both the parasemionotids and the teleosts).

With the exception of the toothed rostral, all these differences are relatively minor, and there is a large number of important characters which *Ichthyokentema* shares with both *Pholidophorus* and *Leptolepis*, showing that *Ichthyokentema* is undoubtedly a member of the Halecostomi. These halecostome characters¹ include the pattern of the sensory canals on the skull roof, the large dermopterotic, the presence of a large supraoccipital and autopterotic, the absence of a surangular in the mandible, the single suborbital, the well ossified vertebrae and the form of the caudal fin. The rhombic scales, with peg and socket articulations, a layer of ganoin, and with bone cells and canals of Williamson (cf. *Pholidophorus higginsii* (Gardiner, 1960 : 317)), and the fulcral scales place *Ichthyokentema* in the Pholidophoriformes rather than in the Leptolepiformes.

Ichthyokentema is therefore a member of the Pholidophoriformes which differs from the Pholidophoridae in one important feature, the toothed rostral separating

¹ While discussing the characters of Halecostomi, it should be mentioned that the characters of this group listed by Saint-Seine (1949 : 299) include, in contrast to holosteans, the general absence of a basiptyergoid process, the absence of a gular and the general absence of suborbitals; and, in contrast to teleosts, the presence of an extrascapular. In fact, none of these characters is typical of halecostomes. The only halecostome in which the basiptyergoid process is definitely lost is *Eoprotelops* (Saint-Seine, 1949 : 262); a gular is apparently always present in halecostomes (pholidophorids, leptolepids, oligopleurids, archaemenids, *Ichthyokentema*); a single suborbital is present in all halecostomes in which the cheek is known except *Pholidophorus segusianus* (Saint-Seine, 1949 : 222), where it is fused with an infraorbital; the extrascapular is present in all but a few specialized teleosts.

the premaxillae, and a number of less important characters including the extensive contact between the nasals, the four supraorbitals, the primitive mandible with a fully ossified Meckel's cartilage, a toothed coronoid and an oral pit-line, the strong palatal dentition, the angle of the suture between the opercular and subopercular and the form of the pedicel of the basisphenoid. All these characters are primitive (see below, p. 34), and *Ichthyokentema* could not therefore have evolved from the Pholidophoridae, yet its late age excludes it from the ancestry of the latter group. Thus *Ichthyokentema* must represent a phyletic line independent of the Pholidophoridae, and it must be placed in a separate family Ichthyokentemidae, defined as on p. 6 above.

(b) *The Origin and Evolution of the Halecostomi*

Ichthyokentema purbeckensis is only the third halecostome in which the neurocranium has been described, and in few halecostomes is the skeleton known in any detail. Detailed information on the structure of *I. purbeckensis*, especially on the characters in which it differs from *Pholidophorus*, make it necessary to discuss the history of the Halecostomi.

(i) *The Origin of the Halecostomi*

Gardiner (1960 : 347) has recently discussed the origin of the halecostomes (= Pholidophoroidea) and has produced much evidence indicating that the group originated from the Eotriassic Parasemionotidae (a family variously classed as advanced sub-holosteans or primitive holosteans), as had been suggested by Saint-Seine (1949 : 292) and by Schaeffer & Dunkle (1950 : 25). Gardiner mentions sixteen points of similarity between the Parasemionotidae and the Pholidophoridae (as represented by *Pholidophorus bechei* and *P. similis*). *Ichthyokentema* agrees with both the parasemionotids and pholidophorids in all these characters except the angle of the suture between the opercular and subopercular and the two postcleithra, in both of which it resembles the parasemionotids rather than the pholidophorids. The differences between *Ichthyokentema* and the Pholidophoridae are listed on p. 32 above. *Ichthyokentema* agrees with the parasemionotids in eight of these ten differences, the characters of the operculum and postcleithra mentioned above, the wide contact between the nasals, the large number of supraorbitals, the presence of a single coronoid and an oral pit-line in the mandible, the strong dentition of the palate, and the presence of canals for the internal carotids in the pedicel of the basisphenoid. *Ichthyokentema* differs from both the parasemionotids and pholidophorids in only one of the ten characters, the absence of an aortal groove or canal below the occipital part of the neurocranium. The major difference between the pholidophorids and *Ichthyokentema* is the presence in the latter of a toothed rostral which separates the premaxillae. Gardiner (in press) discusses the history of the bones of the snout in actinopterygians, and shows that the rostral, the premaxillae and the antorbitals are all derived from the rostro-antorbito-premaxillary of primitive palaeoniscoids such as *Stegotrachelus*, a bone which bears teeth, the rostral

commissure and the junction between the supra- and infraorbital sensory canals. This single bone has fragmented in different ways in different lines, and has given rise to various combinations of snout bones. The presence in *Ichthyokentema* of a median rostral bearing both teeth and the ethmoid commissure is thus a primitive feature recalling the chondrosteans (though no chondrostean has yet been described in which there is both a toothed rostral and a pair of premaxillae). The condition in *Pholidophorus* and *Leptolepis*, with toothed premaxillae meeting beneath a toothless rostral, could be derived from the condition in *Ichthyokentema* by the premaxillae of the latter shifting medially until they excluded the rostral from the border of the mouth and so made its teeth redundant, or it could be derived independently from the primitive palaeoniscoid condition by the fragmentation of a toothed rostro-premaxillary. There is a third possibility, that the condition in *Ichthyokentema* was derived from that in *Pholidophorus* by the premaxillae shifting laterally so that the rostral entered the border of the mouth and acquired teeth secondarily. This must be discarded, firstly because there is no evidence that the rostral has ever acquired teeth secondarily, and secondly because there are eight characters in which *Ichthyokentema* resembles the parasemionotids and differs from *Pholidophorus*, and these eight characters must be taken to be primitive, while there is only a single character, the absence of an aortal canal, in which *Ichthyokentema* is more advanced than *Pholidophorus*; the structure of the snout in *Ichthyokentema* is therefore much more likely to be primitive than it is in *Pholidophorus*. In the Parasemionotidae Lehman (1952 : 167) finds that some specimens of *Watsonulus eugnathoides* have a rostro-premaxillary and others have separate rostral and premaxillae, but does not say whether or not this rostro-premaxillary is paired or median. Piveteau (1941 : 73) describes a median rostral in *W. eugnathoides*, but is uncertain if the premaxillae are paired. In *Parasemionotus* Piveteau (1935 : 146) describes similar conditions, a median rostral and premaxillae which may or may not be paired. Thus it is still uncertain if there was a median rostro-premaxillary in the parasemionotids, but only if there was could both the pholidophorids and *Ichthyokentema* be derived from this family.

Leaving the structure of the snout aside, Gardiner (1960) has given a good account of how the halecostome viscerocranium could be derived from the parasemionotid, but he does not deal with the neurocranium. As *Ichthyokentema* is only the third halecostome in which the neurocranium is known, it is worth discussing some aspects of the evolution of the neurocranium in halecostomes. The parasemionotid neurocranium is known in *Ospia*, *Broughia* (Stensiö, 1932), *Parasemionotus* and *Watsonulus* (Lehman, 1952). The neurocrania of these four genera differ from those of the halecostomes *Pholidophorus*, *Leptolepis* and *Ichthyokentema* in the following characters.

1. The cranial fissure, absent in halecostomes, is present in all parasemionotids, though in *Ospia* both the vestibular fontanelle and the ventral part of the fissure (below the vagus foramen) are closed, and the fissure is not known to extend on to the roof of the neurocranium in any parasemionotid.
2. The parasemionotid neurocranium is normally ossified in a single piece, though in *Ospia* and *Watsonulus* there is the beginning of fragmentation into

separate bones with the separation of a basisphenoid and an orbito-pleurospenoid in the hind wall of the orbit.

3. A fossa bridgei is present in the parasemionotids, and there is a spiracular canal opening into the floor of the fossa. In halecostomes there is no fossa bridgei or spiracular canal, but there is a large post-temporal fossa.

4. In parasemionotids the facial foramen did not open into the pars jugularis, but into the hinder part of the orbit, and the hyomandibular trunk of the facial nerve passed postero-laterally across the wall of the orbit to traverse the pars jugularis from end to end.

5. In parasemionotids the orbital artery was given off from the internal carotid after the latter had traversed its foramen in the parasphenoid (i.e. anterior to the ascending process of the parasphenoid), and the artery passed up through the myodome, entering the medial wall of the pars jugularis in *Parasemionotus* and *Watsonulus*, and failing to enter the pars jugularis at all in *Ospia*.

The first three of these five characters of parasemionotids are typical of chondrosteans, and give the neurocranium a palaeoniscoid appearance. The first two of the differences between parasemionotids and halecostomes are not of great importance, for the cranial fissure and vestibular fontanelle were evidently beginning to close in the parasemionotids, and in *Pholidophorus* the neurocranium is more or less completely ossified (Rayner, 1948 : 322). Rayner (1951 : 77) has suggested that closure of the cranial fissure in holosteans is associated with the increased mechanical function of the region of the neurocranium above the vagus foramen, where the intercalar and post-temporal fossa are developed. This is supported by the presence in *Pachycormus* of a cranial fissure (Lehman, 1949 : 29), as this fish is one of the very few holosteans in which the intercalar is not present.

The absence of a fossa bridgei and a spiracular canal in halecostomes is a real difference between them and the parasemionotids. The fossa bridgei is a depression in the dorsal surface of the otic capsule which lies lateral to the anterior and posterior semicircular canals and dorsal to the external semicircular canal, and is covered by the dermal bones of the skull roof. The fossa is present in all known chondrosteans, though in *Kentuckia*, the most primitive palaeoniscoid in which the neurocranium is known, the fossa is represented only by a group of pits (Rayner, 1951 : 78). The fossa is normally absent in holosteans. The function of the fossa is unknown, and in living chondrosteans it is filled with adipose tissue. Rayner (1951 : 79) has suggested that the fossa is functionless, but as Lehman (1958 : 2082) notes, the constancy of its structure is against this. The spiracular canal and the foramen of the otic branch of the facial nerve normally open into the floor of the anterior part of the fossa, and the foramen of the supratemporal branch of the glossopharyngeal nerve normally opens into its posterior part. The relationship between the fossa and the spiracular canal is not yet clear : Nielsen (1942, 1949) appears to hold that the depression on the roof of the neurocranium into which the spiracular canal opens is always part of the fossa bridgei, whether or not this depression is confluent with the main part of the fossa, while Rayner (1951) suggests that the spiracular canal is not necessarily associated with the fossa. There is a tendency for the fossa bridgei to divide into two in many chondrosteans ; in such forms the spiracular canal and

the foramen of the otic nerve open into the anterior division of the fossa, and the foramen of the supratemporal nerve opens into its posterior division.

Stensiö (1925 : 27) has suggested that the fossa bridgei is homologous with the post-temporal fossa (temporal groove) of holosteans and teleosts. He is supported by Piveteau (1935 : 95). Stensiö was of the opinion that the fossa primitively housed the anterior epaxial trunk muscles, as does the post-temporal fossa, and that the muscles had secondarily withdrawn from the fossa in such forms as living chondrosteans and *Saurichthys*, where a large cranio-spinal process is developed for muscle insertion. This opinion is now untenable since in all the most primitive palaeoniscoids, where the cranio-spinal process is absent or very small, the fossa bridgei is closed posteriorly, and could not have served for muscle insertion. Topographically, the post-temporal fossa agrees almost exactly with the posterior division of the fossa bridgei : it lies lateral to the posterior semicircular canal, dorsal to the external semicircular canal, it is covered primitively by the dermal roofing bones, and often, as in *Ichthyokentema*, the foramen of the supratemporal branch of the glossopharyngeal nerve opens into its floor. Furthermore, no fish is known in which both the posterior division of the fossa bridgei and a well developed post-temporal fossa are present. In spite of these facts, it seems probable that the post-temporal fossa is a new formation which has displaced the fossa bridgei, and has not developed from the latter. Among parasemionotids, the course of the supratemporal nerve is known only in *Ospia* (Stensiö, 1932 : 237). In this genus the nerve, passing upwards from the glossopharyngeal foramen, perforated the lateral wall of the otic capsule to emerge in a shallow depression on the posterior face of the capsule, crossed this depression, and then perforated its roof to emerge in the posterior part of the fossa bridgei. The shallow depression on the posterior face of the otic capsule must, as Stensiö (1932 : 234) says, have served for the insertion of trunk muscles. In the advanced sub-holostean *Perleidus stoschiensis* the supratemporal nerve pursued a similar course (Stensiö, 1932 : 198). The depression on the hind wall of the otic capsule in *Ospia* and *Perleidus* has the same topographical relations as both the posterior part of the fossa bridgei and the post-temporal fossa (lateral to the posterior semicircular canal, dorsal to the external semicircular canal, and perforated by the supratemporal nerve) but it resembles the post-temporal fossa rather than the fossa bridgei in being open posteriorly and in having served for muscle insertion. The evidence suggests that the post-temporal fossa is derived from the shallow depression on the hind wall of the otic capsule of advanced sub-holosteans. Whether, as the post-temporal fossa increased in size by extending forwards, it became confluent with the fossa bridgei is not known, but Rayner (1951 : 78) thinks that the lateral cranial canal of the furid *Caturus*, a canal enclosed within the wall of the otic capsule and communicating with the cranial cavity, is derived from the posterior part of the fossa bridgei, which has already acquired a connection with the cranial cavity in the palaeoniscids *Pteronisculus* and *Boreosomus* (Nielsen, 1942). If this is so, one can imagine the post-temporal fossa increasing in size by pushing its anterior wall forwards, and so overgrowing and enclosing the posterior division of the fossa bridgei.

The anterior part of the fossa bridgei is normally associated with the dorsal

opening of the spiracular canal. The spiracular canal is closed in all halecostomes and teleosts, but is open in the holosteans *Caturus* (Rayner, 1948 : 296), *Pachycormus* (Lehman, 1949 : 27) and *Amia*. The anterior division of the fossa bridgei has not yet been recognized in any holostean, but it is perhaps represented by the group of pits on the dorsal surface of the neurocranium of *Caturus* into which the spiracular canal opens (Rayner, 1948 : 296). Both the spiracular canal and the fossa bridgei were evidently lost very early in the halecostome line, but whether the loss of the fossa was associated with the closure of the spiracular canal is not yet known.

The fourth and fifth of the differences between the neurocrania of parasemionotids and halecostomes listed above appear to be due to specialization in the parasemionotids. In halecostomes, in teleosts, and in all known palaeoniscoids the facial foramen opens directly into the pars jugularis, and the hyomandibular trunk of the facial nerve traverses the jugular canal to emerge posteriorly either with the jugular vein or (primitively) through a separate lateral foramen. The condition in parasemionotids, where the hyomandibular trunk passed across the hind wall of the orbit (in *Watsonulus* the nerve passed through a secondary canal in this wall) before traversing the pars jugularis, is peculiar, and must be considered as a specialization. A similar arrangement occurs in the furid *Osteorachis* (Gardiner, 1960 : 287), and might support the derivation of furids from parasemionotids, but to derive the halecostomes from the parasemionotids makes it necessary to assume that in them the course of the hyomandibular trunk has reverted secondarily to the primitive palaeoniscoid type from the parasemionotid type.

The orbital artery in palaeoniscoids, in halecostomes (known only on *Ichthyokentema*), and in teleosts, leaves the internal carotid on the ventro-lateral face of the otic capsule, before the internal carotid passes through the parasphenoid (i.e. posterior to the ascending process of the parasphenoid), and passes dorso-medially to enter the pars jugularis, primitively passing through a separate foramen in the ventro-lateral wall of the latter, but never entering the myodome. The condition in parasemionotids, where the orbital artery was given off after the internal carotid had passed through the parasphenoid, traversed the myodome, and entered the medial face of the pars jugularis (or, as in *Ospia*, failed to enter the pars jugularis at all) must again be considered as specialized, and if we derive the halecostomes from the parasemionotids we must assume that the apparently primitive course of the orbital artery which they exhibit has been arrived at secondarily.

To sum up this discussion of the origin of the halecostomes, the parasemionotids are almost ideal intermediates between the chondrosteans and holosteans, but two features of the parasemionotid neurocranium, the course of the facial nerve and of the orbital artery, suggest that the group was not directly ancestral to the halecostomes. The snout of parasemionotids is not well known, but only if it contained a median rostro-premaxillary could the conditions in both *Pholidophorus* and *Ichthyokentema* be derived from it. If we accept that the parasemionotids were not directly ancestral to the halecostomes, it is no longer necessary to believe that the halecostomes did not appear until during or after the Eotrias, and it is then easier to account for the presence of the leptolepids, which are among the most advanced halecostomes, as early as the Middle and Upper Trias (Gardiner (personal communi-

cation) confirms that the Middle Triassic specimen mentioned by Rayner (1937 : 46) is indeed a leptolepid, and states that the age of *Leptolepis africana* Gardiner (1960 : 314) is definitely Upper Triassic).

(ii) *The Evolution of the Halecostomi*

Arambourg & Bertin (1958 : 2196) classify the Halecostomi in three orders, the Pholidophoriformes, Leptolepiformes and Aspidorhynchiformes. The aspidorhynchids are highly specialized forms which are not closely related to the other two orders (Gardiner, 1960 : 363), and whose origins are unknown : they may be left aside in the present discussion. The Leptolepiformes contains three families, the Leptolepidae, Oligopleuridae and Protelopidae. The derivation of the leptolepids from the Pholidophoridae is well established (Rayner, 1948 : 338). The Oligopleuridae and Protelopidae are not well known, but none of their known characters excludes the leptolepids from their ancestry, and at present the Leptolepiformes appears to be a monophyletic order derived from the Pholidophoridae. The Pholidophoriformes contains six families, the Pholidophoridae, Pleuropholidae, Archaeomaenidae, Ligulellidae, Majokiidae and Ichthyokentemidae. Detailed knowledge of the skeleton of *Ichthyokentema* makes it necessary to review the relationships of these families.

It is shown above (p. 34) that the structure of the snout in *Ichthyokentema* differs markedly from that of *Pholidophorus*, and that it is unlikely that the *Ichthyokentema* type of snout was derived from the *Pholidophorus* type because *Ichthyokentema* is more primitive than *Pholidophorus* in all but one of the characters in which it differs from the latter. The detailed similarities between *Ichthyokentema* and *Pholidophorus*, especially in those characters in which they both differ from the Parasemionotidae (ossification of the neurocranium in separate and identical bones, presence of a post-temporal fossa, absence of a spiracular canal and cranial fissure, structure of the cheek and vertebrae) make it unlikely that the two should have had an entirely separate origin. The evidence suggests, therefore, that despite its Purbeckian age, *Ichthyokentema* exhibits a primitive halecostome structure, especially in the snout, and that the pholidophorids must either have evolved from a Triassic form similar to *Ichthyokentema*, or have evolved independently from some form in the neighbourhood of the Parasemionotidae. Thus throughout the Jurassic there must have been two separate lines of halecostomes, one with a toothed rostral separating the premaxillae and one with a toothless rostral excluded from the border of the mouth by the premaxillae. It is worth examining the other four families of Pholidophoriformes to discover if any of them show signs of relationship to the ichthyokentemids rather than the pholidophorids.

The Pleuropholidae, a family characterized by deepening of the flank scales, duplication or triplication of the lateral line, and a small, toothless mouth which may have been protrusile, are described by Saint-Seine (1949 : 249 ; 1955 : 79). The family contains three genera, *Pleuropholis*, *Parapleuropholis* and *Austropleuropholis*. All three genera occur in freshwater deposits of Kimeridgian age in the Congo, and *Pleuropholis* also occurs in the marine Kimeridgian and the Lower Cretaceous of Europe. In *Parapleuropholis* Saint-Seine describes the snout as

containing a toothed rostral, a postrostral bearing the ethmoid commissure, and a pair of nasals which are in contact in the mid-line. But since the bone which bears the ethmoid commissure is by definition a rostral, and since Saint-Seine saw no premaxillae, the conditions here suggest that the toothed bone is really the fused premaxillae. In *Pleuropholis*, Saint-Seine's account of the two species *P. thiolleri* and *P. janotti* shows marked differences in the snout. In *P. thiolleri* there is a pair of large, toothless premaxillae, a pair of small rostrals in which no sensory canal or pit-line has been seen, and a pair of nasals separated by the frontals. In *P. janotti* the nasals are separated by a median bone which Saint-Seine calls a postrostral, but no ethmoid commissure and no rostral or premaxillae have been seen. Similarly, in *Austropleuropholis* a postrostral is described, but no ethmoid commissure, rostral or premaxillae have been seen. Biese (1927: 88) has described two species of *Pleuropholis* from the Kimeridgian lithographic stone of Bavaria. In *P. pompecki* he describes paired premaxillae, a median rostral (called the nasal) carrying the ethmoid commissure and paired nasals (called prefrontals) which are separated by the frontals. In *P. wagneri* he finds the same conditions except that the premaxillae are fused. The condition of the snout in the Pleuropholidae, so far as it is known, suggests that the family is derived from a pholidophorid type, with fusion of the premaxillae in *Parapleuropholis* and *Pleuropholis wagneri*, and fragmentation of the rostral in *Pleuropholis thiolleri*. None of the other known characters of the family is against its derivation from the pholidophorids.

The family Archaeomaenidae contains four genera, *Archaeomaene*, *Aphnelepis*, *Aetheolepis* and *Madariscus*, from Australian freshwater deposits of Jurassic age. The family is described by Wade (1941). Both Wade and Gardiner (1960: 352) suggest that the family is derived from the Pholidophoridae, and this is borne out by the structure of the snout. The archaeomaenid snout is known in *Archaeomaene* and *Aphnelepis*, and in both genera there is a median rostral bearing the ethmoid commissure, the premaxillae are in contact below the rostral, and the nasals are in contact in the mid-line; this is the typical pattern of the snout in a primitive pholidophorid. The four archaeomaenid genera appear to fall into two groups. In *Aetheolepis* and *Aphnelepis* the scales are rhombic and deepened on the flank (as in many species of *Pholidophorus*), and the second infraorbital below the dermosphenotic is enlarged (as in *Pholidophorus segusianus* (Saint-Seine, 1949: 222), though the suborbital is here fused with the enlarged infraorbital). In *Archaeomaene* and *Madariscus* the scales are thin and cycloid, and the third infraorbital below the dermosphenotic is enlarged (as it is in *Pholidophorus bechei* (Rayner, 1948: 320)). Unusual features of the Archaeomaenidae as described by Wade are the presence of a surangular in the mandible of *Aphnelepis* and the presence of a pit-line on the preopercular in *Archaeomaene*. Both these characters are typical of chondrosteans, and if they are in fact present would indicate that the archaeomaenids originated independently from forms like the parasemionotids, where a surangular and an unfragmented preopercular are still present.

The Majokiidae is a monotypic family containing *Majokia brasseyi* Saint-Seine (1955: 107), a species known only by two specimens from the Kimeridgian freshwater beds of the Congo. Saint-Seine describes the snout of the species as containing a median rostral, a pair of lateral rostrals, a median postrostral and a pair of large

nasals which are separated through the greater part of their length by the postrostral. No trace of the ethmoid commissure has been seen, and although toothed maxillae are present no premaxillae are known. We have insufficient information to decide if Saint-Seine's postrostral is a true postrostral (as it would be if the ethmoid commissure lay on the rostral), or if his lateral rostrals are toothless premaxillae; depending on the interpretation of the snout bones the species could be derived from either the pholidophorid line or the ichthyokentemid line, or independently from the parasemionotids by fragmentation of a median rostro-premaxillary.

The Ligulellidae is another monotypic family containing *Ligulella sluyisi* (Saint-Seine, 1955 : 103) from the freshwater Kimeridgian of the Congo. The species is poorly known, and the only bone which has been described in the snout is a massive, projecting rostral which bears teeth along both sides. Once again, the ethmoid commissure has not been seen, and no premaxillae are known. The species could be derived from the ichthyokentemid line by increase in size of the rostral, or from the pholidophorids by fusion and increase in size of the premaxillae.

To sum up this discussion of the relationships of the Pholidophoriformes, the order contained at least two lines, the pholidophorid and ichthyokentemid, differing in snout structure. The pholidophorid line could have evolved from the ichthyokentemids or could have arisen independently from the parasemionotids. The ichthyokentemids are more primitive than the pholidophorids and could not have evolved from them. The pholidophorid line gave rise to the Leptolepiformes, from which the teleosts are derived. The pleuropholids probably arose from the pholidophorid line. The archaemaenids are similar to the pholidophorids in snout structure, but they exhibit two primitive characters which suggest that they may be an independent line from a parasemionotid-like ancestor. The majokiids and ligulellids are poorly known, but both could be derived either from the pholidophorids or the ichthyokentemids.

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VIII. LETTERING USED IN THE TEXT-FIGURES

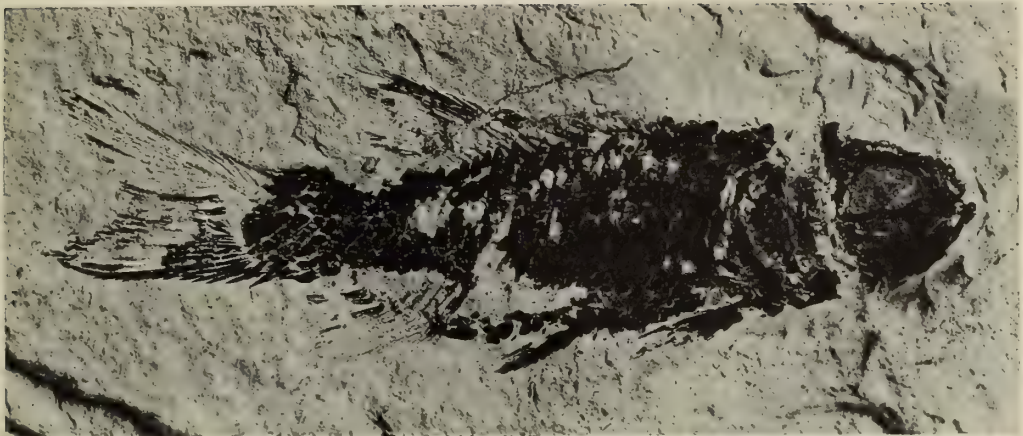
ang.	angular	M.b.	Meckelian bone
ao.	antorbital	mcor.	mesocoracoid arch
a.p.cor.	anterior process of coracoid	mes.	mesethmoid
apto.	autopterotic	mpt.	metapterygoid
aspo.	autosphenotic	mx.	maxilla
b.h.c.	bucco-hypophysial canal	mx.p.p.	maxillary process of palatine
bo.	basioccipital	myo.	myodome
bpt.p.	basipterygoid process	na.	nasal
br.	branchiostegal ray	n.ap.	narial aperture
bs.	basisphenoid	neu.	neural arch
c.i.c.a.	canal for internal carotid artery	omp.	oralo-mandibular pit-line
cl.	cleithrum	op.	opercular
cor.	coronoid bone	op.p.	opercular process of hyoman-
d.ch.	distal ossification of ceratohyal		dibular
den.	dentary	ors.	orbitosphenoid
d.f.	dilatator fossa	pa.	parietal
d.pcl.	dorsal postcleithrum	pas.	parasphenoid
dp.to.	dermopterotic	p.ch.	proximal ossification of cerato-
dspo.	dermosphenotic		hyal
ecp.	ectopterygoid	pf.	profundus foramen
enp.	endopterygoid	pls.	pleurosphenoid
epo.	epiotic	pmx.	premaxilla
esc.	extrascapular	pop.	preopercular
exo.	exoccipital	p.p.cor.	posterior process of coracoid
f.a.c.v.	foramen of anterior cerebral vein	pro.	prootic
f.d.n.	foramen of diazonal nerve	pro.b.	prootic bridge
f.e.ps.a.	foramen of efferent pseudo-	p.t.f.	post-temporal fossa
	branchial artery	q.	quadrate
f.f.	facial foramen	ro.	rostral
f.hm.	facet for articulation of hyo-	sc.f.	scapular foramen
	mandibular	scl.	supracleithrum
f.i.c.a.	foramen of internal carotid	smx.	supramaxilla
	artery	so.	supraorbital
f.ih.	facet for interhyal	soc.	supraoccipital
f.l.e.	articular facet for lateral eth-	sop.	subopercular
	moid on palatine	ssc.	suprascapular
f.m.	foramen magnum	sub.	suborbital
f.o.a.	groove for orbital artery	sym.	symplectic
f.o.n.	foramen of occipital nerve	t.f.	trigeminal foramen
f.ot.n.	foramen of otic nerve	t.p.	transverse process
fr.	frontal	vo.	vomer
f.st.IX	foramen of supratemporal branch	v.pcl.	ventral postcleithrum
	of glossopharyngeal nerve	I	foramen of olfactory nerve
f.vo.	articular facet for vomer on	II	optic fenestra
	palatine	III	notch for oculomotor nerve
g.h.a.	groove for afferent pseudo-	V mand.	canal for division of mandibular
	branchial artery		branch of trigeminal nerve
gl.f.	glenoid facet	VI	foramen of abducens nerve
g.p.	gular plate	VII hm.	foramen for hyomandibular
hm.	hyomandibular		trunk of facial nerve
ic.	intercalar	VII lat.	foramen for lateralis branches of
io.	infraorbital		facial nerve
iop.	interopercular	VII p.	course of palatine nerve
l.	lachrymal	IX	glossopharyngeal foramen
l.e.	lateral ethmoid	X	vagus foramen

PLATE I

Ichthyokentema purbeckensis (Davies)

FIG. 1. Complete fish. P. 8378. \times 1.8.

FIG. 2. Head showing medial surface of cheek bones of the right side. P. 1073. \times 4.5.



1



2

PLATE 2

Ichthyokentema purbeckensis (Davies)

FIG. 3. Skull lacking ethmoid region in dorsal view. P. 44949. $\times 5.5$.

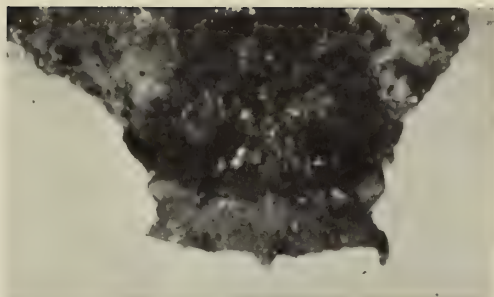
FIG. 4. Anterior end of neurocranium in dorsal view, to show rostral. P. 44927. $\times 15$.

FIG. 5. Snout region in lateral view, to show the nasal (na.), rostral (ro.) and premaxilla (pmx.). P. 8379. $\times 8.5$.

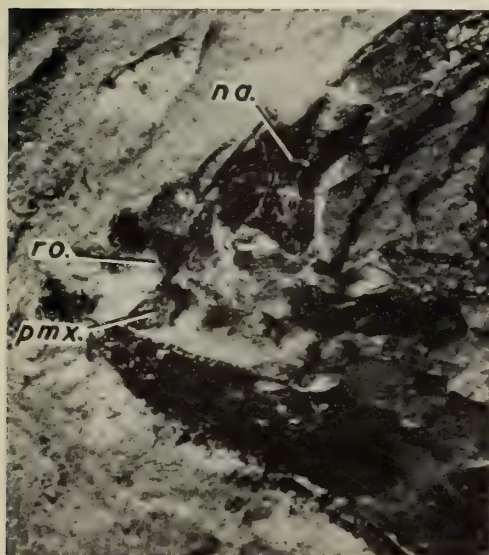
FIG. 6. Photomicrograph of flank scale in optical section, to show bone cell spaces and canals of Williamson (c.W.). P. 45031. $\times 360$.



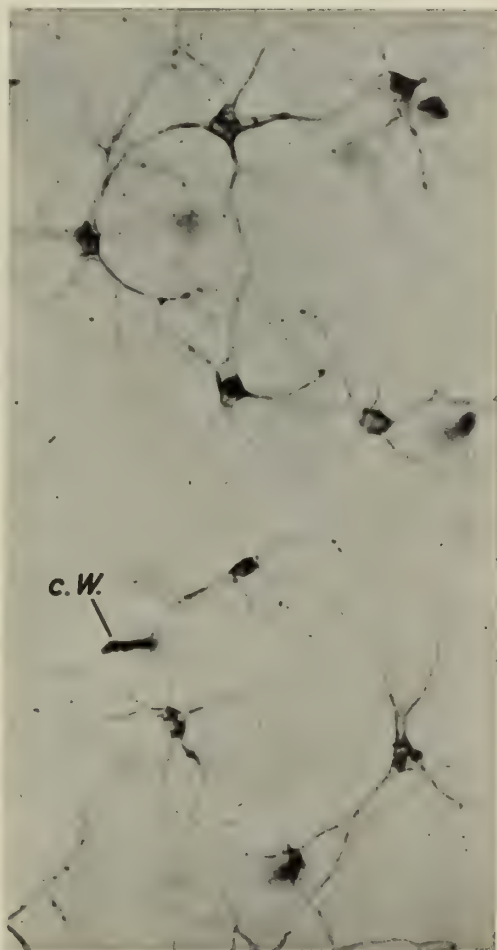
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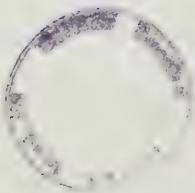
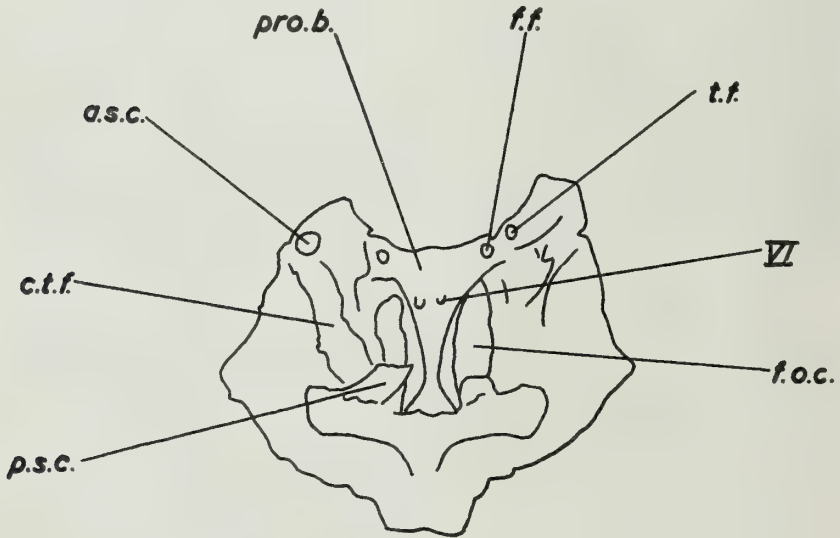
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PLATE 3

Ichthyokentema purbeckensis (Davies)

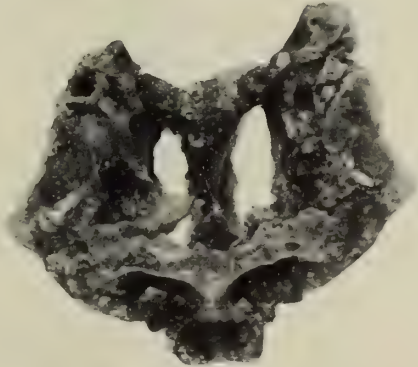
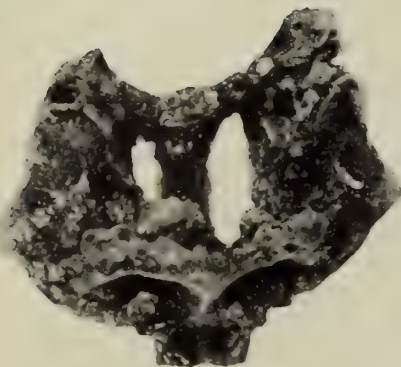
FIG. 7. Stereoscopic pair of neurocranium in ventral view. P. 44929. $\times 6.5$.

FIG. 8. Stereoscopic pair of incomplete neurocranium in dorsal view, to show the cranial cavity : a.s.c. ; anterior semicircular canal in prootic : c.t.f. ; space, filled in life by cartilage, in the floor of the post-temporal fossa : f.f. ; facial foramen : f.o.c. ; fenestra between the cranial cavity and the otolith chamber : pro.b. ; prootic bridge : p.s.c. ; posterior semicircular canal in epiotic : t.f. ; trigeminal foramen : VI ; abducens foramen. P. 44934. $\times 8$.





7



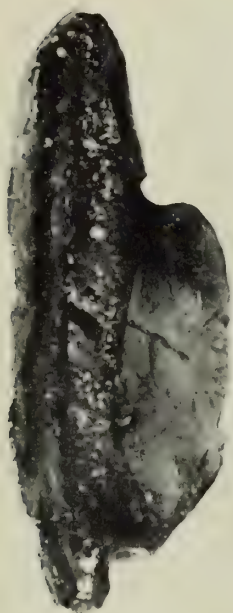
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PLATE 4

Ichthyokentema purbeckensis (Davies)

FIG. 9. Stereoscopic pair of mandible of the right side in medial view. P. 44974. $\times 9.5$.

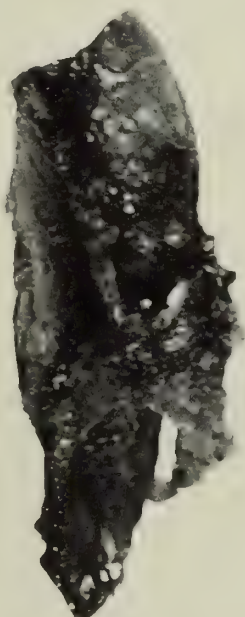
FIG. 10. Stereoscopic pair of endoskeletal pectoral girdle and incomplete cleithrum of the right side in medial view. P. 44967. $\times 9.5$.

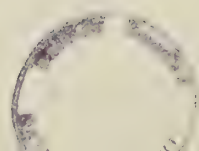


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A NEW MESOZOIC FLORA FROM
TICÓ, SANTA CRUZ PROVINCE,
ARGENTINA



S. ARCHANGELSKY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY

Vol. 8 No. 2

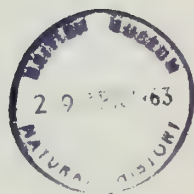
LONDON : 1963

A NEW MESOZOIC FLORA FROM TICÓ,
SANTA CRUZ PROVINCE, ARGENTINA

BY

SERGIO ARCHANGELSKY

(Museo de Ciencias Naturales, La Plata, Argentina)



Pp. 45-92 ; 12 Plates ; 79 Text-figures

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A NEW MESOZOIC FLORA FROM TICÓ, SANTA CRUZ PROVINCE, ARGENTINA

By SERGIO ARCHANGELSKY

SYNOPSIS

The present paper is the first contribution to our knowledge of the newly discovered Ticó flora from Santa Cruz Province, Argentina. Six fern-like fronds and a small fruit are referred to five new genera, *Ticoa*, *Ruflorinia*, *Mesodescolea*, *Mesosingeria* and *Ktalenia*. The conifers consist of four new species of *Brachyphyllum* (*B. brettii*, *B. mucronatum*, *B. irregulare* and *B. mirandai*) the last-named species being associated with small male cones probably belonging to the *Araucariaceae*. The cuticle of *Athrotaxis ungeri* (Halle) is described for the first time and a new genus, *Tomaxellia*, with a single species, *T. degiustoi*, is based on sterile cutinized twigs of uncertain systematic position. The age of the flora is probably Upper Jurassic or Lower Cretaceous.

I. INTRODUCTION

DURING the 1957 Palaeobotanical Expedition to Patagonia, sponsored by the Lillo Institute, Dr. J. M. de Giusto (geologist of the YPF National Oil Company) conducted Mr. R. Herbst and the writer to a recently discovered fossiliferous locality in the centre of Santa Cruz Province, Argentina. The main exposures occur in the Magdalena Estancia in a semicircular cliff (*barranca* in Spanish) and it is here proposed to include all the exposures which belong to a uniform group of sediments, probably of fluvial origin, under the name Ticó Amphitheatre.

Only a few specimens of fossil plants were collected from two fossiliferous beds during this first short visit. The specimens were subsequently found to be very well preserved compressions and a further expedition was undertaken during the summer of 1958 when a more thorough survey was made and at least a dozen new fossiliferous beds were discovered in the Amphitheatre. Towards the north, the same formation was found to constitute the main exposure in an area covering many square miles. To the east it was possible to trace a lateral correlation with the lowermost part of the Baqueró Formation, in the classical area of Punta del Barco and Cerro Cuadrado, composed of white tuffs with good impressions of *Hausmannia*, *Gleichenites*, *Cladophlebis* etc. There is little doubt that a vast sedimentary basin exists in this part of Santa Cruz Province and it is hoped that a thorough study of the fossil flora will help to determine its age. Present incomplete evidence points to its being between Upper Jurassic (and very likely post-Kimmeridgian) and Lower Cretaceous. The complete absence of Angiosperms tells against an Upper Cretaceous age.

The first part of this paper deals with a small group of gymnospermous plants and the second part with Conifers. Dr. C. A. Menéndez (Buenos Aires) is presently studying the Bennettitales from the same flora with a view to publication in the near future.

II. SYSTEMATIC DESCRIPTIONS

GYMNOSPERMAE

The species described below may well have been placed in form-genera such as *Sphenopteris* and *Pecopteris*, at least in the comprehensive way in which they were once used. But as much more information than the shape of the pinnules is available in the present material, the fact that they are gymnospermous leaves can be clearly demonstrated and a whole series of new genera is needed for them. Their affinities are most likely to be with the Cycads in the strict sense or with the Pteridosperms.

It is interesting to note that some of the genera described (e.g. *Ticoa*, *Mesodescolea*) possess stomata very similar to those of Recent Cycadales. *Ktalenia circularis* gen. et sp. n., a fructification, is included below because it is closely associated with *Ruflorinia sierra* gen. et sp. n., and was seen only where this plant occurs.

Genus *TICOA* nov.

DIAGNOSIS.—Leaf large, up to tripinnate with robust main rachis. Primary and secondary pinnae laterally attached at angle of 45° . No pinnules between pinnae on primary rachis. Pinnules of pecopteroid type, slightly decurrent, usually concrescent at their base, sometimes overlapping. One vein entering each pinnule, in large pinnules giving off lateral veinlets and in small pinnules forking once at an acute angle.

Cuticle varying in thickness from 2.5 to $8\ \mu$ (measured in folds); upper cuticle usually thicker than lower. Stomata few or absent on upper cuticle. All cells elongated on upper cuticle; lower cuticle with elongated cells on margins and on veins, more or less elongated cells between the veins, becoming isodiametric or wedge-shaped around the stomata. Cell walls straight, not interrupted by pits. Cell surface normally flat. Cells on rachises markedly elongated. Trichomes and papillae may be present.

Stomata mainly on lower cuticle with few on the upper; those on lower cuticle avoiding veins and margins; concentration in intermediate areas 9–30 per sq. mm. Guard cells rather large ($50\ \mu$ long) orientated with longitudinal axis parallel with veins, sunken in a large pit; pit oval or round, formed by subsidiary cells and one or more series of encircling cells. Mouth of pit formed by 8–14 outer encircling cells.

DISCUSSION.—The genus *Ticoa* is based on two species found in different beds of the Ticó Amphitheatre. Both species possess well-preserved cuticles. *T. harrissii* is an important constituent of the floral assemblage in Ticó and is dominant in one bed together with *Ruflorinia sierra*.

If form and venation alone were considered the leaves could have been included in *Pecopteris* (or *Cladophlebis*), but the facts provided by the cuticles warrant more precise taxonomic treatment. The polycyclic stomata with large round pits are more like those of such Cycadales as *Cycas revoluta* or *Dioon edule* than any other living or fossil plants, and *Ticoa* is here classified provisionally as near the Cycadales in the strict sense. It has rather different stomata from certain other living Cycads and the presumed fossil ones such as *Ctenis* and *Pseudoctenis*. It must also be admitted that the distinction between "presumed fossil Cycads" and "presumed Mesozoic Pteridosperms" is vague but *Ticoa* has no close resemblance in stomata to any "presumed Pteridosperm" yet described.

TYPE SPECIES.—*Ticoa harrisii* sp. n.

***Ticoa harrisii* sp. n.**

(Pl. 1, figs. 2, 5; Pl. 2, fig. 7; Pl. 4, figs. 15, 16, 20; Text-figs. 1, 2, 9–13)

DIAGNOSIS.—In part of leaf known, leaf tripinnate, up to 16 cm. wide. Main rachis 8 mm. wide with slight longitudinal striae. Primary pinnae laterally inserted at an angle of 45° , subopposite, separate or slightly overlapping, over 10 cm. long, 2 cm. wide, linear lanceolate; rachises 2 mm. wide, bearing two distinct flanges on the upper surface near the edges. Secondary pinnae typically 15 mm. long, 5–6 mm. wide, inserted at an angle of 45° , alternate; the first arises near the main axis on the catadromic side. Secondary pinnae as a whole lanceolate, slightly overlapping adjacent pinnae; secondary pinnae ending in an acute pinnule. Pinnules up to 3 mm. \times 1.6 mm., slightly decurrent, lanceolate with broad base. Those towards distal part of pinnae rather acute. Those towards proximal part of pinnae (near rachis) broader, having alternate, slightly marked lobes. Each pinnule with a single vein; vein simple or forked once at an acute angle. No small pinnules occurring on the main primary rachises.

Upper cuticle, $3.5\ \mu$, slightly thicker than lower ($2.5\ \mu$ measured in folds) having almost no stomata but numerous trichomes; cells elongated, parallel to the margins. Lower cuticle with elongated cells near margins and on veins, somewhat isodiametric or wedge-shaped near stomata and trichomes, slightly elongated on rest of lamina; cells often placed in groups side by side, showing late division. Surface of cells normally flat but a very few bearing an inconspicuous median papilla. Cuticle of rachises with very long cells and abundant trichomes, smaller than in lamina with few markedly elongated stomata. Small round papillae may be present. Cell walls of both cuticles conspicuous, straight, not interrupted by pits; cell surface flat, without any visible markings.

Stomata dicyclic, usually avoiding veins and margins, orientated with long axis parallel to veins and margins, 25–30 per sq. mm. Guard cells strongly sunken in round or oval pit, 15–30 μ deep, formed by subsidiary cells and encircling cells. Encircling cells usually 8–10, conspicuous, forming sides of pit typically 40–50 μ wide and mouth of pit typically 30–40 μ wide. Mouth of pit round or irregular, situated at same level as epidermis; subsidiary cells small and inconspicuous at bottom of pit; guard cells typically 50 μ long, with small area of cutinised surface



Ticoa harrisii gen. et sp. n.

FIG. 1. General aspect of the holotype. LIL 2538. $\times 1$.

FIG. 2. Normal pinna of same. $\times 2.5$.

Ticoa magnipinnulata sp. n.

FIG. 3. Portion of pinna from holotype. LIL 2540. $\times 1$.

FIG. 4. Apical part of pinna. LIL 2541. $\times 1$.

FIGS. 5, 6. Portions of pinnae. LIL 2540. $\times 2.5$.

near aperture and at poles. Trichomes single, sometimes in pairs, 45–55 per sq. mm., consisting of basal granulate cell, 25 μ wide in exposed part, but with inwardly extending cutinised walls enlarging to 35–40 μ wide, surrounded by about 5 ordinary epidermal cells. Free part only known as a short tube of cuticle about 20 μ wide.

HOLOTYPE.—LIL PB n.2538.

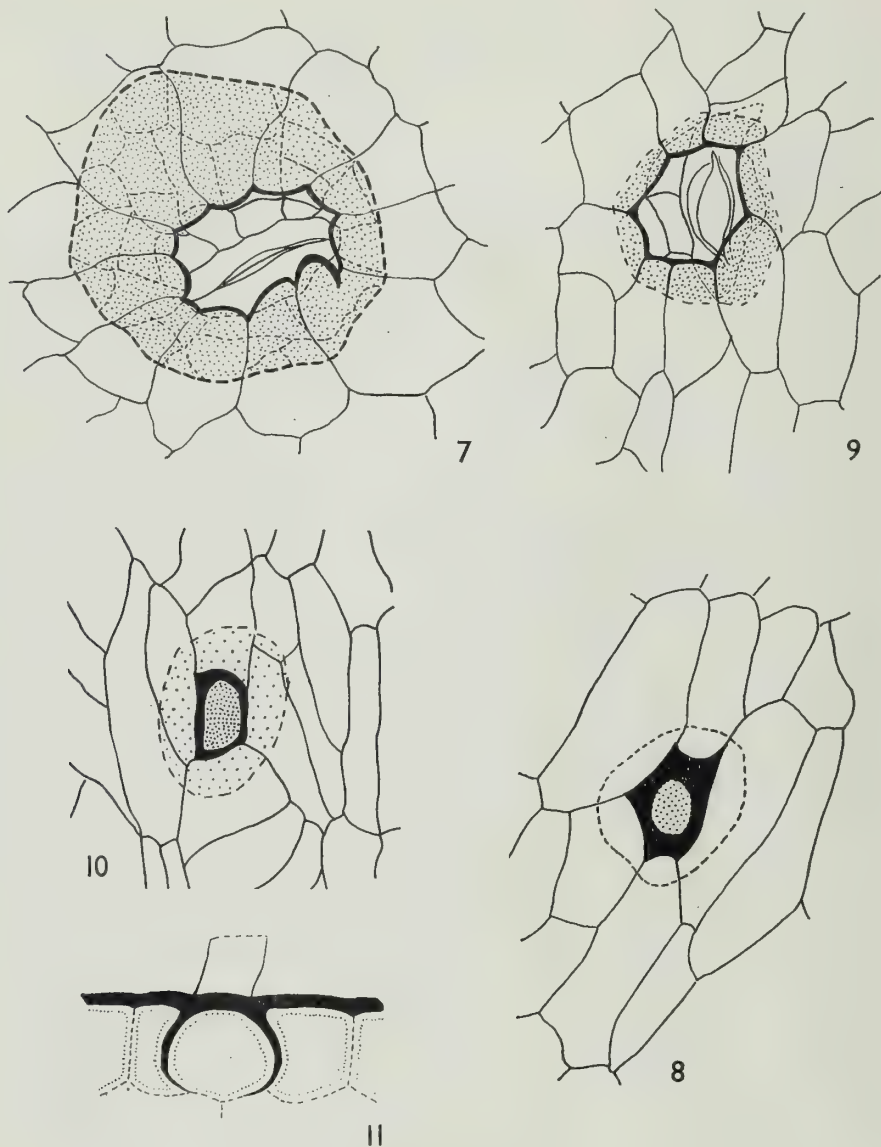
MATERIAL.—In addition to the holotype, LIL PB n.2539; Brit. Mus. (Nat. Hist.) Palaeontological Dept., no. V.44660. Slides: LIL 160–164; V.44659.

DESCRIPTION.—The best available specimen is shown in Text-fig. 1 but there are many other fragments and it is one of the commonest species. Well preserved cuticles alone remain as a pale yellow film, the whole interior substance having almost disappeared. The cuticle of the main rachis has fallen off. The veins of the pinnules can only be seen with certainty on the lower cuticle where elongated epidermal cells and the almost complete absence of stomata are the main diagnostic features. Forking of the veins is rarely seen. The upper cuticle is thicker than the lower and in stained preparations this difference in thickness is clearly seen. The lower cuticle shows that on the margins of the pinnules there is a conspicuous zone, devoid of stomata, with elongated cells attaining more than $100 \times 15 \mu$, in up to 10 definite rows. This tendency for elongation in the epidermal cells is noteworthy, for only in areas around the stomata or trichomes can more or less isodiametric cells, about 20–40 μ in diameter, be found. The cell walls are straight, 1 μ thick, and no sinuities have been seen. The depth of the stomatal pits mentioned in the diagnosis can be seen in occasional stomata which have been compressed laterally. It is interesting to note that the mouth of the stoma is usually open. The trichome bases are abundant and remains of trichomes have occasionally been observed. The cell lying under the trichome is always cutinised, but not completely (Text-fig. 11). The anticlinal walls of these cells project inwards at least 10 μ , the extent of this projection being clearly seen in obliquely compressed specimens. There is a marked tendency for the bases to unite in pairs or groups of three. Occasionally small papillae may be seen. The two flanges found on the rachises attain up to 0.4 mm. in width on a rachis 2 mm. wide. They are always folded towards the edges.

DISCUSSION.—The stomata of *Ticoa* look remarkably like those of *Cycas revoluta*. However, in *Cycas* the pore formed by the encircling cells is raised, while in *Ticoa* it is on the same level as the rest of the cuticle. The same difference applies to *Dioon edule* which also has a markedly raised pore. In *Cycas revoluta* and *Ticoa harrisii* there is a conspicuous line dividing the guard cell from the subsidiary cells. The depth of this line is slightly less than that of the aperture of the guard cell. In *Cycas* this line is known to be a sharp fold and looks as if it were a hinge assisting stomatal movement. I have made full use of the stomata of *Cycas revoluta* in my reconstruction of that of *Ticoa harrisii*.

Pseudoctenis lanei Thomas, as figured by Harris (1932: 89, text-fig. 36, I) sometimes has a dicyclic stomatiferous apparatus, being quite similar to *T. harrisii* in this respect. The pit in *P. lanei*, however, is much smaller and the shape of the leaves does not correspond to that of *Ticoa*.

The species is dedicated to Professor T. M. Harris of Reading University.



Ticoa magnipinnulata sp. n.

FIG. 7. Stoma. FIG. 8. Base of trichome. Both from V.44658.

Ticoa harrisii gen. et sp. n.

FIG. 9. Stoma. FIGS. 10, 11. Bases of trichomes. Slide LIL 161.
All $\times 500$.

Ticoa magnipinnulata sp. n.

(Pl. 1, figs. 1, 3, 4; Pl. 2, fig. 6; Pl. 4, figs. 17-19; Text-figs. 3-8, 14-16)

DIAGNOSIS.—(Leaf known from very small fragments only). Pinnae up to 2 cm. wide; rachis 1 mm. wide, flat. Pinnules subopposite, of pectopteroid form; shape oblong, typically 10 mm. long \times 4 mm. wide, margins entire, apex rounded or obtuse, occasionally acute, base broad, lower margin decurrent, angle of insertion 65° ; smaller pinnules relatively shorter, united with their neighbours for about 1 mm. near the base. A midrib arises near lower margin and curves outwards and then remains straight to pinnule apex; lateral veins simple, alternate, first vein on catadromic side arises close to pinna rachis; lateral veins forming angle of 35° with midvein. No small pinnules on primary rachises.

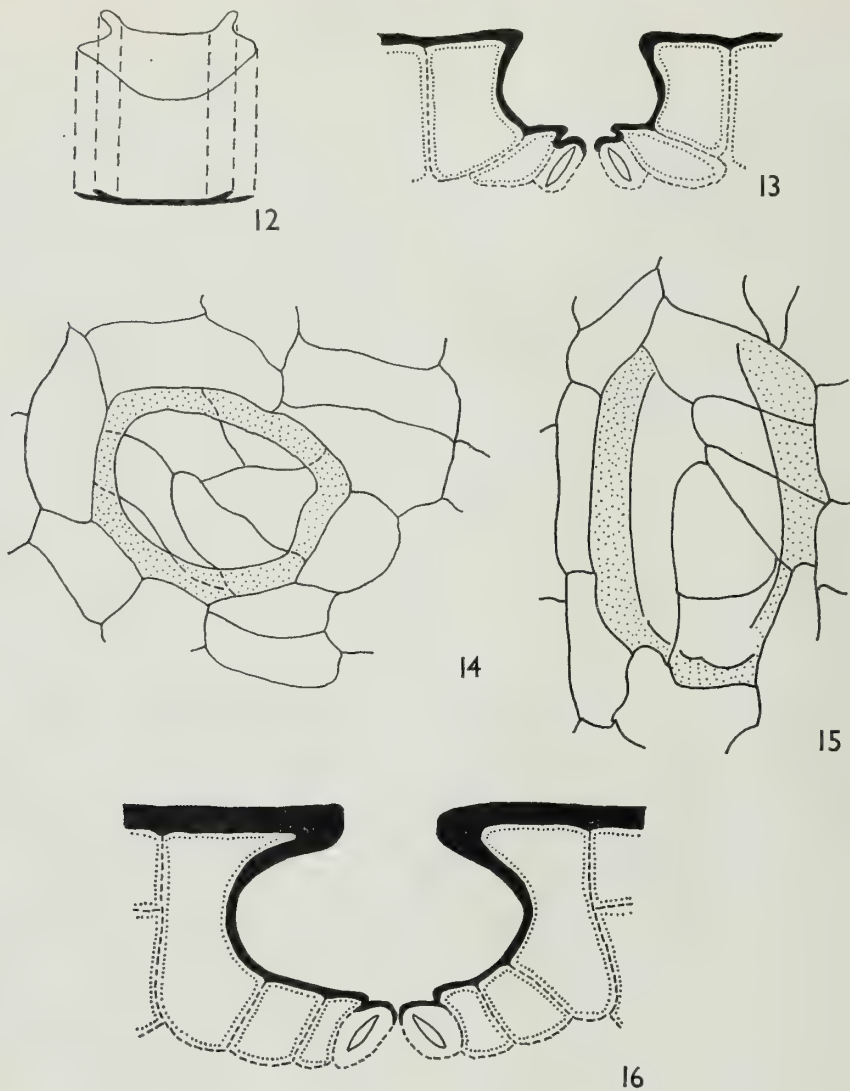
Cuticle of upper side very thick, up to $8\ \mu$, having a darker colour than lower one, bearing numerous trichomes but no stomata. Cells on upper cuticle uniformly elongated, except around trichomes where they are isodiametric. Cells of lower cuticle markedly elongated on margins and on veins, slightly elongated on rest of lamina, more or less isodiametric around stomata; cells sometimes placed in groups side by side, showing late division. Cells on rachis cuticle markedly elongated, having numerous trichomes and few long stomata. Cell walls on both cuticles conspicuous, straight, not interrupted by pits; cell surface flat, without any visible markings.

Stomata confined to lower cuticle, polycyclic, avoiding veins and margins, round or oval with long axis parallel to veins, 9-13 per sq. mm. Guard cells strongly sunken in oval or round pit formed by subsidiary cells, inner encircling cells and one or two series of outer encircling cells. Outermost encircling cells sometimes markedly thickened near mouth of pit, projecting as large inwardly pointing hollow papillae. Mouth of pit typically $50\ \mu$ long \times $30\ \mu$ wide, slightly raised over epidermis, formed by typically 12-14 encircling cells. Subsidiary cells small and inconspicuous at bottom of pit, surrounded by ring of similar encircling cells surrounded by at least one other series of cells, forming the sides of the pit, typically $100\ \mu$ long \times $80\ \mu$ wide, together with outermost encircling cells. Guard cells typically $50\ \mu$ long \times $10\ \mu$ wide. Trichomes single, sometimes in pairs, 20-40 per sq. mm., consisting of a basal granulated cell, $15\ \mu$ wide in exposed parts, but with inwardly extending cutinised walls enlarging to a width of $40\ \mu$, surrounded by 5-6 epidermal cells. Sometimes groups of cells on lower cuticle forming oval structures up to $100\ \mu$ long \times $60\ \mu$ wide, slightly sunken in a pit.

HOLOTYPE.—LIL PB 2540.

MATERIAL.—In addition to the holotype, LIL PB 2541; Brit. Mus. (Nat. Hist.) no. V.44657. Slides: LIL 165-169; V.44658.

DESCRIPTION.—The few specimens referred to this species were found in a different bed from that in which *Ticoa harrisii* occurs. The cuticles are equally well preserved and similar in colour to those of *T. harrisii*. In the few pinnules preserved the veinlets can be clearly seen in translucent preparations but only very obscurely on the rock. They have a typical monopodial arrangement. The specimens of *T. magnipinnulata* agree in their form and cuticle, but one specimen is distinguished



Ticoa harrisii gen. et sp. n.

FIG. 12. Compression of the two rachis flanges. $\times 10$.

FIG. 13. Section of stoma. $\times 500$.

Ticoa magnipinnulata sp. n.

FIGS. 14, 15. Oval structures on lower cuticle, slightly sunken in a pit.

V.44658. $\times 500$.

FIG. 16. Section of stoma. $\times 500$.

from the others by its more acute pinnules and rather fewer stomata and trichomes. They all agree in having no stomata on the upper side and that even the smallest stomata are polycyclic. Certain laterally compressed stomata show the guard cells to be sunken $40\ \mu$ below the general surface level. The trichomes are remarkably small, compared with the size of the stomata, and quite often the inward extension of the cutinised basal cell does not widen very much. Very few groups of two trichomes were seen, most trichomes occurring singly. In one specimen the lower cuticle shows groups of cells of variable size and shape, usually the same size as stomata and forming an oval structure sunken in a pit and sometimes even having a rim of cutin around the large mouth of the pit. The function of these structures is unknown (Text-figs. 14, 15).

DISCUSSION.—*Ticoa magnipinnulata* looks very like *T. harrisii* and the cuticles of both species are also similar, but there are some real differences which are set out below.

	<i>Ticoa harrisii</i>	<i>Ticoa magnipinnulata</i>
Flanges on upper side of rachis	Present	Absent
Pinnules	Lanceolate with broad base. Larger ones crescent. 3 mm. long \times 1.5 mm. wide.	Oblong with broad base. Larger ones separated. 10 mm. long \times 4 mm. wide.
Cuticles	Up to $9.5\ \mu$ thick. Upper with a few stoma. Stomata dicyclic. 25–30 stomata per sq. mm. Mouth of pit 30–40 μ . Same level with epidermis. Encircling cells 8–10. Sides of pit 40–50 μ . Trichomes 45–55 per sq. mm. Basal cell 25 μ (nearly as large as stoma).	Up to 8 μ thick. Upper non-stomatiferous. Stomata polycyclic. 10–13 stomata per sq. mm. Mouth of pit 50–30 μ . Slightly raised. (Outer) encircling cells 12–14. Sides of pit 100–80 μ . Trichomes 30–40 per sq. mm. Basal cell 15 μ (much smaller than in stoma).

Genus *RUFLORINIA* nov.

DIAGNOSIS.—As for the only species, *Ruflorinia sierra* sp. n.

Ruflorinia sierra gen. et sp. n.

(Pl. 2, figs. 8, 9; Pl. 5, fig. 21; Text-figs. 17–20, 24)

DIAGNOSIS.—(For purposes of description leaf assumed to be tripinnate).

Primary pinna at least 8 cm. long, 4 cm. broad. Rachis of primary pinna 2 mm. wide with median groove on upper side with flanges of decurrent, lamina 0.3 mm. wide. Secondary pinnae alternate to subopposite, decurrent, insertion angle 45° , linear, with acute apex, up to 45 mm. long \times 4–5 mm. wide; lamina of one pinna separated from next by narrow gap; pinna rachis with slight median longitudinal



17



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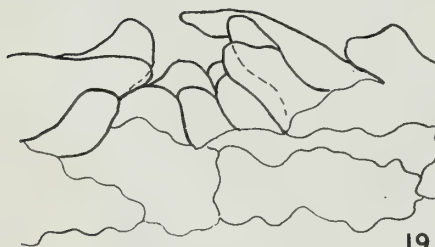
21



18



22



19



23

Ruflorinia sierra gen. et sp. n.

FIG. 17. Section of stoma. $\times 450$.

FIG. 18. Stoma. Slide LIL 170. $\times 450$.

FIG. 19. Lateral view of compressed stoma, showing papilla-like projections of the subsidiary cells. Slide LIL 171. $\times 500$.

FIG. 20. Details of pinna, showing venation. LIL 2565. $\times 5$.

Mesodescolea plicata gen. et sp. n.

FIG. 21. Section of stoma. $\times 500$.

FIGS. 22, 23. Stomata showing cuticular ridges. Slide LIL 177. $\times 500$.

groove and laminate margin. Pinnules concrescent at their base or up to half their length, with lanceolate acute apex, inserted at an angle of about 25° , measuring up to 4 mm. long \times 1.5 mm. wide. A single vein enters the pinnules, forking once near base at acute angle, and again, sometimes twice, near middle of lamina. No small pinnules on primary rachises.

Upper and lower cuticle same thickness, $1-2 \mu$; upper cuticle devoid of stomata. Cell walls sinuous on both cuticles, sharply marked, not interrupted by pits, cells on margins and veins elongated, near stomata somewhat isodiametric. On rachises and main veins, cells very long, narrow, rectangular, having less sinuosities. Cell surface normally flat; cells with occasional hollow papillae only found around stomatal region.

Stomata dicyclic or polycyclic, avoiding veins and margins, disposed in marked longitudinal rows, usually occurring in small groups, with long axis orientated in long axis of pinnules; about 10 stomata per sq. mm. Guard cells on same level as epidermis or slightly sunken in round or oval pit formed by numerous subsidiary and encircling cells. Subsidiary cells rather small, forming bottom of pit; polar subsidiary cells often elongated and narrow. Inner encircling cells (if present) small, forming sides of pit typically 75μ in diameter when round. Outer encircling cells, typically 14-18 in number, forming sides and top of round or oval pit, often extending onto epidermal surface; cuticle becoming thickened in part near stoma and raised to form large hollow papilla; papillae often completely united to sides of adjacent papilla so that whole set of papillae form a raised rim overhanging stomatal pit; opening between papillae often narrow. Polar encircling cells often long and narrow. Guard cells typically 50μ long, with oval thickened area round mouth of stoma, up to 40μ long \times 5μ broad.

HOLOTYPE.—LIL PB 2542 (a).

MATERIAL.—In addition to the holotype, LIL PB 2544, 2545, 2549, 2550(a), 2551, 2552, 2554-56, 2565(b), 2567(b), 2570(b), 2575(b); Brit. Mus. (Nat. Hist.) nos. V.44676-77, V.44686, V.44681-82. Slides: LIL 170-172; V.44678-80.

DESCRIPTION.—*Rufloflinia sierra* is found in close association with *Ticoa harrisii*. It is, however, easily distinguishable from this species by the different shape of the pinnules and thinner cuticle. The cuticle is brownish yellow and when detached leaves a brown impression on the matrix. The details of such impressions are usually better preserved than those of *T. harrisii*. Being much thinner, the cuticle is not as well preserved as that of *T. harrisii*, but reasonably good preparations can be made without much difficulty. The leaf was probably tripinnate but the present material studied does not provide conclusive evidence that this was so.

The concrescence of the pinnules is noteworthy and in distal parts of the pinnae only their apices are separated; the shape then suggests that of a saw (*sierra* in Spanish). The veins often bifurcate three times and the ultimate veinlets can reach the apex or lateral margins of the pinnules. The absence of stomata on the upper cuticle and on the rachises is consistent. On the lower cuticle the stomata are usually present in quite definite rows, tending to form groups or patches composed of up to 5-6 stomata together. Large areas of the lamina are devoid of stomata and so it is not easy to establish with accuracy their number per sq. mm. which in any case is

extremely low. The stomata vary greatly in size from moderate to extremely large, and the mouth of the pit is closed in some but wide open in others. There are a



FIG. 24. *Ruflorinia sierra* gen. et sp. n. General aspect of the holotype. LIL 2542. $\times 1$.

FIG. 25. *Mesosingeria herbstii* sp. n. Holotype. LIL 2546. $\times 1$.

FIGS. 26-28. *Mesodescolea plicata* gen. et sp. n. 26, Holotype. LIL 2548. $\times 1$. 27, 28, Non-differentiated pinnae. $\times 2.5$.

FIGS. 29-31. *Mesosingeria coriacea* gen. et sp. n. 29, 30, Fragments of the holotype. LIL 2547. $\times 1$. 31, Another fragmentary pinna. LIL 2558. $\times 1$.

few stomata in which the whole apparatus is $110\ \mu$ long, which is rather exceptional in plants of any family. The walls of the subsidiary and encircling cells form a complex network around the guard cells. A very constant feature is the tendency for the polar subsidiary and encircling cells to be elongated in the longitudinal axis of the pinnules. There may be one, or sometimes two, subsidiary cells approximately opposite each pole of the guard cell, but a single polar encircling cell is found opposite the pair if there are two. This indicates a late radially orientated division in the polar subsidiary cell.

DISCUSSION.—*Ruflorinia* has remarkable characters which clearly distinguish it even from genera of rather similar habit. *Ticoa* is the most similar genus in being repeatedly pinnate and having polycyclic stomata. *Ruflorinia*, however, differs in its sinuous cell walls, the grouping of stomata in patches and in the papillae of the outer encircling cells which project over the mouth of the pit.

The genus is dedicated to Professor Rudolf Florin, Stockholm, Sweden.

Genus *MESODESCOLEA* nov.

DIAGNOSIS.—As for the only species, *Mesodescolea plicata* sp. n.

Mesodescolea plicata gen. et sp. n.

(Pl. 3, figs. 12–14, Pl. 5, figs. 24, 25 ; Text-figs. 21–23, 26–28)

DIAGNOSIS.—Leaf bipinnate, oblong, typically 6 cm. long \times 4 cm. wide. Leaf rachis less than 1 mm. wide with deep longitudinal midfurrow. Pinnae opposite, decurrent, arising at 30° to rachis, lanceolate, with rather narrow base, up to 4–5 cm. long \times 1.5 cm. wide near middle and ending with single acute pinnule. Pinna rachis with pronounced midfurrow. Pinnules subopposite to alternate, arising at 30° to pinna rachis ; pinnules with broad base and acute apex, up to 15 mm. long \times 3 mm. wide, margins entire ; lower margin markedly decurrent and connecting with upper margin of pinnule below. An unbranched midrib enters pinnules and extends to near apex.

Upper cuticle without stomata. Cells polygonal, square or rectangular, up to $40\ \mu$ long \times $30\ \mu$ wide. Anticlinal walls usually pitted, up to $3\ \mu$ thick. Cell surface usually with ridges having no definite orientation. Cuticle of lower surface having stomata except on veins. Cells on veins elongated, with conspicuous longitudinal ridges. Cells on lamina of irregular shape, usually with rounded contours ; anticlinal walls about $2\ \mu$ thick, pitted. Cell surface with irregular ridges. Specialised small cells (trichome bases) present, surrounded by conspicuous series of radiating ridges which cross up to several rows of surrounding cells. Ridges at right angles or parallel to long axis of stomata, also conspicuous.

Stomata on lower cuticle typically monocyclic, oval or nearly round, with no definite orientation, typically 23–35 μ long, 45–60 per sq. mm. Guard cells little or not at all sunken. Subsidiary cells not specialised, from 5–8, usually bearing

ridges which can be normal or parallel to long axis of stoma. Guard cells with a conspicuous and constant rim surrounding mouth, sometimes interrupted at poles. Contact of guard cells and subsidiary cells generally covered by strong ridge reproducing roughly the outlines of guard cells.

HOLOTYPE.—LIL PB n. 2548.

MATERIAL.—In addition to the holotype, LIL PB 2550(b); Brit. Mus. (Nat. Hist.) no. V.44682-83. Slides: LIL 177-180; V.44684-85.

DESCRIPTION.—This species is associated with *Ticoa harrisii* and *Ruflofinia sierra*. It is generally found in fragments which leave only a faint impression on the rock, but the rachis impression is distinct and marked with strong furrows. The cuticle although well preserved is difficult to prepare in large pieces. The lower cuticle is yellowish while the upper is darker and brownish in colour.

On the same block containing the holotype, near the base of the leaf, a cutinised rachis is preserved and although there is no definite evidence of actual connection it may well belong to *Mesodescolea*. The rachis is 5 mm. wide, having a thick cuticle with elongated cells; the cell walls are pitted and 4 μ thick. The cell surface is covered with conspicuous longitudinal ridges.

The difference in the shape of the cells on the upper and lower cuticles is evident, as is the lack of stomata or trichomes on the upper cuticle. However, both cuticles bear conspicuous ridges which are a constant feature of the species.

The guard cells of the stomata always have the rim of thickened cutin surrounding the mouth. Usually, a ridge is present on the edge of the guard cell, and sometimes there is another longitudinal ridge in between the two thickened zones. No trichomes or hairs have been seen, but the specialized small cells with concentric radiating ridges, occupying large areas of the lamina are presumably the bases of trichomes.

Certain leaf fragments were also found that might well be small undifferentiated pinnae or rather large pinnules with three apical horns.

DISCUSSION.—*Mesodescolea plicata* is a remarkable fossil. The leaf somewhat resembles certain species of *Pachypteris* in shape, for instance *P. dalmatica* Kern (see Carpentier, 1927, pl. 12, figs. 13, 14). Certain Angiosperms too have leaves of similar outline, although quite a different type of venation. The cuticle has some features in common with the living Cycad *Stangeria*, in particular, the surface striation or ridges, but these are stronger in *Mesodescolea* (cf. Thomas & Bancroft, 1913, pl. 17, fig. 2). The stomata in both plants are unspecialized, the guard cells being on the same level with the epidermis or a little sunken. The thickenings round the aperture of the guard cells as well as the polar and lateral ridges on the margins of the guard cells are comparable; in *Mesodescolea* these ridges are generally fused to form a continuous rim of cutin and are also stronger than in *Stangeria*. The cells of the lower and upper cuticles of *Stangeria* have sinuous walls and no pits. The cells on the veins of both plants are also comparable; they are elongated and have strong longitudinal ridges. In spite of all these similarities, however, there is considerable difference in branching and venation, and while one may provisionally classify *Mesodescolea* in or near the Cycadales it can only be with reservation. This is equally true of the relation between *Ticoa* and *Cycas* or *Dioon*.

There are certain similarities with *Ctenis minuta* Florin (1933, text-fig. 22, c; pl. 11, fig. 5) in the cuticular ridges and the radiating striae from trichome bases. *C. kaneharai* Yokoyama, however, bears the greatest resemblance to *Mesodescolea* as far as the cuticular structure is concerned. This species was first described from the Upper Cretaceous of Japan, but neither Yokoyama nor Oishi gave any description of the cuticle. Harris (1950) described some specimens from the Jurassic of Yorkshire with cuticles preserved and I was able to compare the Yorkshire cuticles with that of *Mesodescolea*. The Yorkshire cuticle is intensely marked with ridges as in the Ticó specimens (more than in *Stangeria*), there are similar trichome bases and the stomata are present only on the lower cuticle. In *C. kaneharai*, however, the stomatal apparatus is more protected and somewhat sunken in an oval pit. The guard cells have no thickenings and the stomata of *Mesodescolea*, in this respect, are closer to those of *Stangeria*.

As in the case of *Ticoa*, one can assume that *Mesodescolea* also is a Gymnospermous plant, having certain features in common with the living *Stangeria paradoxa* on the one hand, and with some fossil *Ctenis* species on the other. *Mesodescolea* probably belongs to a stock of plants with cycadean affinities, which existed in Patagonia during Upper Mesozoic times, before the appearance of a true angiospermous flora.

The genus *Mesodescolea* is dedicated to Dr. Horacio Descole, Tucumán, Argentina.

Genus **MESOSINGERIA** nov.

DIAGNOSIS.—Leaf bipinnate. Pinnae ovate or lanceolate ending with a single pinnule. Pinna rachis flat. Pinnules oblong to lanceolate, margins entire, angle of insertion 45° – 50° , alternate; base narrower than middle of lamina and lower margin slightly decurrent. One or more veins enter pinnule, each forking once or twice at acute angle, all branches going straight up to near apex.

Cuticle thick. Stomata present on both cuticles, more frequent on lower. Epidermal cells on both cuticles typically isodiametric, slightly elongated on margins. Cells on rachises rectangular or square. Veins not distinguishable on either cuticle. Cell walls strongly marked, straight, with visible middle lamella and border. Cell surface flat, finely granular.

Stomata monocyclic, often with longitudinal orientation. Guard cells strongly sunken in round or oval pit formed by typically 5–8 unspecialised subsidiary cells. Mouth of pit raised over surface of epidermis, constricted by more or less continuous rim of cutin. Trichome bases present.

TYPE SPECIES.—*Mesosingeria coriacea* sp. n.

DISCUSSION.—This genus is based on two species, rather incompletely preserved, but sufficiently well to make a clear generic separation from other fossil leaves known at present.

Mesosingeria differs from the fern-like leaves described above as *Ticoa*, *Ruflorinia*, and *Mesodescolea*. In the general shape of the leaves and in the thick cuticle, *Mesosingeria* can be compared with *Pachypteris* and *Pachydermophyllum*, the cuticles of which are rather similar, having more or less isodiametric epidermal cells, thick walls and sunken guard cells. But in *Mesosingeria* the subsidiary cells

do not project over the mouth of the pit like papillae (Thomas & Bose, 1955, text-fig. 3, E). Instead there is a more or less continuous round rim of cutin raised over the general surface of the lamina. This peculiar feature is also found in species of *Ctenozamites* (cf. *Ctenopteris*) such as *C. leckenbyi* or *C. cycadea* (Harris, 1961, text-fig. 2, B). However, there are other features which do not agree with *Mesosingeria*. In *Ctenozamites* the veins are distinct on both lower and upper cuticles and the stomata are usually confined to the lower side; also, the epidermal cells are not as isodiametric as in *Mesosingeria*. In *Pachypteris* and *Ctenozamites* there are pinnules on the main rachis, between the pinnae, while they are absent in *Mesosingeria*.

It seems probable that *Mesosingeria* is related to *Pachydermophyllum-Pachypteris* and belongs to the Mesozoic Gymnosperms, probably Pteridosperms (*sensu lato*).

Another similar plant is Saporta's *Scleropteris* (1873: 364). I have examined specimens in the Paris Museum but could not find any evidence of cuticle and the question of any relationship between *Mesosingeria* and *Scleropteris* must therefore remain unanswered.

The genus is dedicated to Professor Rolf Singer, Buenos Aires, Argentina.

Mesosingeria coriacea gen. et sp. n.

(Pl. 3, fig. 10; Pl. 5, figs. 22, 23; Text-figs. 29-33, 37, 38)

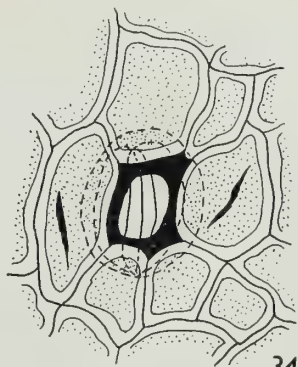
DIAGNOSIS.—(For purposes of description, leaf assumed to be bipinnate). Pinnae up to 4 cm. long \times 1.5 cm. wide, ending with single obtuse pinnule; pinna rachis flat, up to 2.5 mm. wide. Pinnae apparently overlapping. Pinnules oblong with rounded apex, touching each other, inserted at an angle of 45° to pinna rachis, alternate, typically 1 cm. long \times 0.4 cm. wide with margin entire; base narrower than middle of lamina; upper margin contracted and lower margin slightly decurrent. One or more veins enter the pinnule, each forking once or twice at very acute angle, all branches going straight up to near apex; all veins of same thickness. Margins quite flat.

Cuticles on both sides thick, up to 7 μ . Stomata present on both cuticles but more abundant on lower. Cells on both cuticles isodiametric or slightly elongated, typically 40 μ in diameter; cells on margins rather elongated; cells on rachis rectangular or square. Veins not distinguishable on either cuticle. Cell walls very strongly marked, consisting of a cutinised middle lamella (anticlinal walls) extending up to 50 μ inwards. At surface, middle lamella accompanied by strongly marked border about 8 μ wide. Surface of cell (periclinal walls) flat, finely granular.

Stomata typically 60-70 per sq. mm. on lower cuticle, and less than 5 per sq. mm. on upper. Stomata monocyclic, nearly all with longitudinal orientation on lower side, but varied on the upper. Guard cells sunken strongly in a pit; pit up to 60 μ in diameter with thickly cutinised walls, often constricted by typically 5-7 unspecialised subsidiary cells. Mouth of pit rounded or elongated, up to 50 μ wide, raised over surface of lamina. Mouth of pit further constricted by very delicate, more or less continuous projection of cutin, pierced by a round hole. Hole with distinct border. Guard cells moderately cutinised, typically 90 μ long \times 30 μ wide. Hypo-



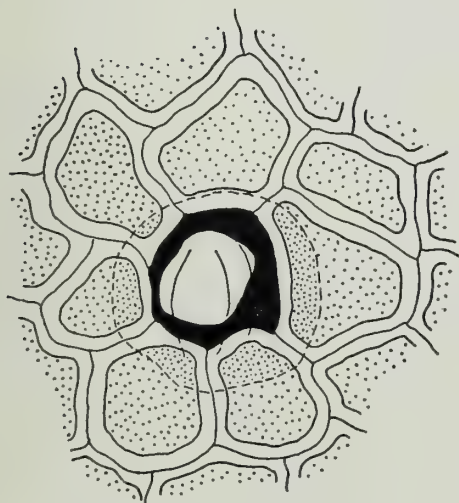
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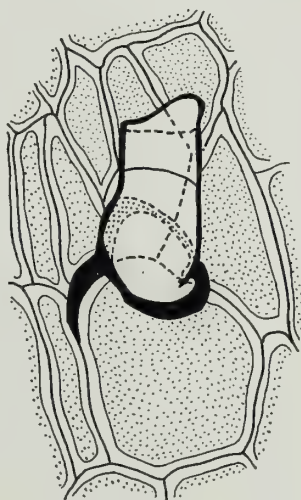
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36

Mesosingeria coriacea gen. et sp. n.

FIG. 32. Base of hair. Slide LIL 173.

FIG. 33. Stoma with rim of cutin round the mouth of the pit. Slide LIL 173.

Mesosingeria herbstii sp. n.

FIG. 34. Stoma without projecting rim of cutin. Slide LIL 175.

FIG. 35. Section of stoma.

FIG. 36. Bicellular hair. Slide LIL 175. All $\times 500$.

dermal cells often cutinised, in contact with guard cells of stomata, smaller than epidermal cells.

Trichome bases present in small numbers on both sides, consisting of a round cell about $50-60\ \mu$ in diameter on top of normal epidermal cells; trichome bases sometimes consisting of two cells sharing a thin area. Free part of trichome missing.

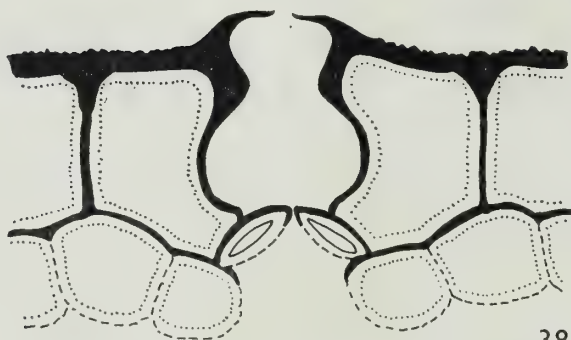
HOLOTYPE.—LIL PB n. 2547.

MATERIAL.—In addition to the holotype, LIL PB 2558. Slides: LIL 173, 174; Brit. Mus. (Nat. Hist.) nos. V. 44665-66.

DESCRIPTION.—This species is found in the same bed with *Ticoa magnipinnulata* and *Mesosingeria herbstii*. The dark-brown cuticles are very well preserved. The largest specimens required much longer maceration than the rest of the material



37



38

Mesosingeria coriacea gen. et sp. n.

FIG. 37. Stoma showing sunken guard cells. Slide LIL 173. $\times 500$.

FIG. 38. Section of stoma showing projecting rim of cutin over the mouth of the pit and cutinized hypodermal cells. $\times 500$.

hitherto studied. The impressions show generally clear contours with marked veins. Although the holotype is fragmentary, several pinnae having a parallel course appear to originate from a common rachis. It is for this reason that the leaf is assumed to be at least bipinnate.

With a hand lens the cell contours and the anticlinal cutinised walls are clearly seen. The smaller specimens have a thinner cuticle which needs less maceration, although it is dark brown in colour. The shape of the pinnules and the angle of insertion is the same as in the larger specimens but the pinnules of the smaller ones tend to be more united at the base. Numerous misshapen or crushed cells with dark contents can be seen. They are perhaps pathological.

DISCUSSION.—This species resembles *Pachydermophyllum papillosum* more than the other species described below. Comparison between two specimens, one of *P. papillosum* and the other of *M. coriacea* shows a resemblance in the shape of the pinnules and in the thickness of the cuticle. *Pachydermophyllum*, however, has a single midvein in each pinna (as does *Pachypteris* in each pinnule, except for the terminal lobe where there are a few main veins, representing suppressed pinnules).

Mesosingeria herbstii sp. n.

(Pl. 3, fig. 11; Pl. 5, figs. 26, 27; Pl. 6, fig. 36; Text-figs. 25, 34–36)

DIAGNOSIS. (Leaf only known from fragments). Pinnae up to 1 cm. wide; rachis flat, 1.5 mm. wide, with fine striae. Pinnules lanceolate, separated, alternate, typically 7 mm. long \times 1.5 mm. wide; margins entire with definite flange; apex acute, base narrower than middle of lamina; lower margins slightly decurrent, angle of insertion about 40°.

Upper cuticle, 4 μ , thicker than lower cuticle. Stomata present on both cuticles, more abundant on lower one. Cells on both cuticles isodiametric, typically 20–25 μ in diameter, slightly elongated on margins. Veins not distinguishable on either cuticle. Cells on rachis elongated rectangular, having several hairs and papillae. Cell walls straight, strongly marked, projecting slightly outwards and more strongly inwards, inward part occasionally interrupted by pits. Cell surface normally flat, very finely granular, showing several obscure striae. Occasional cells bearing hollow papilla; some cells, especially near margins, bearing hairs of 1–2 cells, strongly cutinised for whole length, 60 μ long \times 20 μ wide. Cells on smargin and apex strongly cutinised and often projecting as small tooth. Stomata on upper cuticle about 40 per sq. mm., on lower cuticle about 110 per sq. mm., often with longitudinal orientation, not forming rows. Stomata typically monocyclic with guard cells sunken in round pit, typically 30 μ wide, formed by 6–8 unspecialised subsidiary cells. Mouth of pit rounded or oval, 8–10 μ wide, constricted by continuous rim of cuticle extending from inner edges of subsidiary cells. Guard cells feebly cutinised, about 30 μ long \times 15 μ wide.

HOLOTYPE.—LIL PB n. 2546.

MATERIAL.—In addition to the holotype, slides LIL 175, 176; Brit. Mus. (Nat. Hist.) no. V. 44664.

DESCRIPTION.—The specimens described here were found in the same bed as *Ticoa magnipinnulata*. The cuticles are well preserved and light yellow in colour. The impressions, although showing clear contours, do not show any trace of veins. In one instance, however, a trace of the midvein appears to be present. The apical parts of the pinnules have conspicuous longitudinal wrinkles or folds in their cutinised surface which suggest veins, but there is no other evidence to confirm that the veins run in this direction. The flanges on the margins are clearly seen and are probably due to the abundant papillae and hairs. The insertion of the pinnules is not exactly lateral, one row seems to overlap slightly onto the rachis.

The lower cuticle is thinner, $2.5\ \mu$, and stains strongly with safranine. The guard cells can be seen only in stomata in which the round rim of strongly cutinised matter is either missing or has fallen off. The guard cells are feebly cutinised and their contours cannot always be made out. The pit is usually a little expanded, but in some cases the lateral walls of the subsidiary cells descend almost vertically.

DISCUSSION.—This species differs from *M. coriacea* in the shape of its smaller pinnules which are more lanceolate and in the colour and thickness of cuticle. The size and shape of the pinnules of the two species can be compared in Text-figs. 25, 29–31. The frequency of stomata on both upper and lower cuticles is higher in *M. herbstii*. All the epidermal features such as cells, stomata and hair bases are also smaller in this species. The numerous hairs present in the marginal regions also constitute a conspicuous character, whereas they are absent in *M. coriacea*, which has no marginal concentration of hairs but only a few trichome bases scattered over the lamina.

Some figured specimens of *Pachypteris lanceolata* Brongniart are similar to this species. Thomas (1954 : 320, text-figs. 1, 2) figures some specimens from Yorkshire which are similar in shape but larger than *M. herbstii*. Vachrameev & Samilina (1958, text-figs. 1, 2) also figure specimens of *Pachypteris* from the Jurassic of Russia which resemble *M. herbstii* although the pinnules are rather broader in the Russian material. The epidermal structure of these leaves, which I have studied from preparations of the Yorkshire material, presents some small differences when compared with that of *M. herbstii*, such as the presence of a definite midrib seen on the lower cuticle, and the dicyclic condition seen in some stomata. On the upper cuticle of *P. lanceolata* there are almost no stomata.

Mesosingeria herbstii shows some resemblance, as far as the external morphology of fronds is concerned, to some species of the genus *Scleropteris*. In the Paris Museum I was able to examine specimens of *S. pomelii* and *S. compacta*. *S. pomelii* (no. 11549 and no. 11555) is only a faint impression with no cuticle or organic matter remaining. The holotype of *S. compacta* Saporta (no. 11507) still retains some organic matter, but it was impossible to make a cuticle preparation. This species has much smaller pinnules than *M. herbstii*. Another species, *S. laevigata*, is missing from the collections. The following species of *Scleropteris* are more or less comparable to *M. herbstii* : *S. phillipsii* (Saporta, 1873, pl. 45, figs. 2, 3) and *S. laevigata* (pl. 46, fig. 3), but in the absence of cuticular structure a reliable comparison cannot be made.

The species is dedicated to Mr. R. Herbst, Tucumán, Argentina.

Genus *KTALENIA* nov.

DIAGNOSIS.—As for the only species, *Ktalenia circularis* sp. n.

The generic name has been taken from the word *Ktalenk*, which in the language of the Tehuelche Indians (Patagonia) means “little”.

Ktalenia circularis gen. et sp. n.

(Pl. 6, figs. 28–33; Text-figs. 39–43)

DIAGNOSIS.—Fruit circular (originally globular), typically 3–4 mm. wide. Surface smooth. (Stalk and pollination opening not distinguished.)

Fruit wall strongly cutinised. Cuticle typically 5 μ thick, but thinner in some areas. Stomata absent. Surface flat, anticlinal cell walls straight, entire, sometimes pitted, cutinised down to hypodermis. Periclinal walls smooth or having granules and reticulation. Cells typically isodiametric, 15–20 μ wide, often elongated, having no definite orientation. Sometimes elongated cells converging radially to a centre occupied by one or two more or less isodiametric cells. Circular bases of trichomes present, usually sited over three or four cells at their corners. Hypodermal cells cutinised, larger than epidermal cells.

One or two seeds enclosed in the fruit. Seeds orthotropous. Integument, nucellus and megaspore membrane cutinised.

Cuticle of integument very delicate, extending from micropylar canal over nucellus, down to base of seed. Cell outlines very feebly marked. Cells somewhat rectangular. One or more small papillae present on cell surface.

Nucellus free, cutinised down to base. Cuticle of nucellus less than 1 μ thick. Largest seeds with nucellus 1.5 mm. long, smallest 0.8 mm. long. Cells of nucellus large, rectangular, typically 100 $\mu \times$ 30–40 μ , becoming small and isodiametric at base of micropylar canal. Cell walls on micropylar canal more strongly cutinised than cells of nucellus, rectangular, with somewhat sinuous walls. Cells near chalaza becoming narrower. Micropylar canal in large seeds (occurring single in a fruit) about 250 μ long \times 140 μ at base, becoming narrower towards top. At base, a round hole, about 150 μ wide, represents the insertion point of nucellus in chalaza.

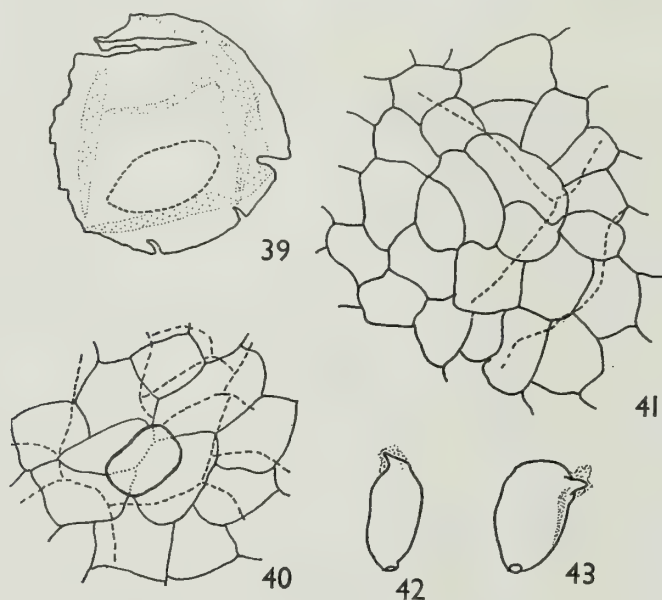
Megaspore membrane usually present, without any definite indication of cells, but a finely granular texture. Numerous round dark brown bodies, about 30–40 μ wide, are enclosed in megaspore membrane. They may correspond to an oily endosperm.

HOLOTYPE.—Slide LIL 181.

MATERIAL.—In addition to the holotype, slides: LIL 181–184; Brit. Mus. (Nat. Hist.) nos. V.44687–89.

DESCRIPTION.—*Ktalenia circularis* is an abundant fossil in the *Ticoa harrisii* bed. Often it is found in association with *Rufloflinia sierra*. It is preserved in two different ways in the same bed. The most complete type of preservation consists of a disc of cuticle enclosing the one or two seeds and a very little coaly matter. In these specimens the seeds do not form any visible bulge on the outside of the fossil. The other form, which is rather commoner, consists of half-fruits. Here, only one

surface shows the fruit cuticle, and the other, the internal surface, shows a hollow which is filled with rock matrix. The hollow is round or slightly oval in shape. These specimens are considered to be the same as the complete ones, because they are of the same size and the cuticles are exactly similar; no seeds have been found in these half-fruits. Between the hollow and the cuticle there is a thick carbonaceous layer, probably corresponding to the stony layer of the fruit wall.



Kialenia circularis gen. et sp. n.

FIG. 39. General aspect of the fruit wall cuticle, showing a single seed inside (broken line). Slide LIL 181, holotype. $\times 10$.

FIG. 40. Cuticle of the fruit wall to show base of a trichome. Slide LIL 182. $\times 500$.

FIG. 41. Fruit wall cuticle showing a group of recently divided cells in the centre. Slide LIL 182. $\times 500$.

FIGS. 42, 43. Schematic drawings of two seeds, showing the cuticle of the nucellus; at the base the circular chalazal insertion, and at the top (dots) remains of the integument around micropylar canal. $\times 10$.

I have so far been unable to discover the stalk or the pollination opening of the fruits, although occasionally fragments of integument cuticle containing circular holes were observed.

The cuticle of the nucellus, when preserved, is easy to prepare. It is more difficult to deal with the integument cuticle. The micropylar canal is not always preserved, probably being broken off during maceration. The megaspore membrane and the endosperm substance are usually but not always preserved. With regard to the origin of the round bodies inside the megaspore membrane, I assume these are the remains of oil reserves which hardened during fossilisation. Their nature could be

similar to the aleurones of *Caytonia* and some other seeds. They are probably preserved because of the protection afforded by the thick cuticle of the fruit wall and the two other cuticles, the integument and nucellus, which are almost closed.

No pollen grains have been seen in the micropylar canal, although some are occasionally present in the preparations, sticking to the cuticles. They are of different types and no attempt has been made to correlate them with the fruits.

DISCUSSION.—For the purpose of description I have assumed these round bodies to be fruits and as more than one seed has been found inside them they may well be true fruits. In this respect the terminology is like that used for the fruit of *Caytonia* or the Angiosperms, but this is not meant to imply close affinities. At present we lack much important data.

It is unfortunate that nothing can be said about the attachment of these fruits, nor about the opening which permitted pollination or fertilization. Clearly both must have existed, but as far as present evidence goes, the cuticle of the fruit forms an almost continuous sac. Some specimens do show small gaps which I believe to be original features, but these gaps cannot be related to one another.

Among Mesozoic seeds which have been described in detail, only *Caytonia* possesses features similar to *Ktalenia* but there are some differences. In *Caytonia* there are usually more than two seeds in the fruit, rarely two. In *Ktalenia* the micropylar canal is directly opposite the top of the nucellus (probably they are fused) as in *Caytonia*. The cuticle of the nucellus of both genera is thicker than that of the outer integument, and there is no evidence of inner integument. The megaspore membrane, present in *Ktalenia*, is missing in *Caytonia* (Harris, 1958).

CONIFERALES

Halle (1913) described, among other fossil plants, some Mesozoic conifers from Patagonia, preserved as impressions. Subsequently petrified cones from what is now known as the Matilda Formation (Middle to Upper Jurassic) were described by several authors in successive contributions (Spegazzini, 1924 ; Gothan, 1925 ; Calder, 1953). Apart from these there are only a few scattered references to Mesozoic coniferous shoots including Menéndez (1956) who described two shoots with poorly preserved cuticle. In the Tertiary, however, several interesting species are known (Florin, 1948).

The specimens described below are compressions in which cuticles are well preserved but almost all the internal coaly matter has disappeared. The cuticles are easily prepared by maceration in HNO_3 plus KClO_3 for a few hours, followed by dilute ammonia.

The present evidence is consistent with the view expressed by Florin (1940) that all known Argentinian Mesozoic Conifers belong to the families Taxodiaceae, Araucariaceae and possibly Podocarpaceae, the last two being represented in the flora today.

Genus *BRACHYPHYLLUM* Brongniart

The four species described below agree generically with the emended diagnosis of

Brachyphyllum given by Kendall (1947) and accepted by Wesley (1956), but the species differ from those of the Northern Hemisphere.

Brachyphyllum is certainly an unnatural assemblage. One species, *B. mamillare* has Araucarian reproductive organs, whilst another, *B. expansum*, has a cone which does not appear to be Araucarian (Kendall, 1949). The foliage of *Cheirolepis muensteri*, if considered alone, would certainly be placed in the genus *Brachyphyllum* but its cones are very different from those of *Araucaria*. It is interesting that a male cone resembling *Araucaria* is associated with *Brachyphyllum mirandai* sp. n., but there is not yet sufficient evidence to relate the cone and the shoots as organs of one species.

Three of the species described here are very similar, and quite probably they belong to one natural genus. There is doubt about the position of the other species, *B. irregulare*, which differs markedly in some diagnostic characters.

Brachyphyllum brettii sp. n.

(Pl. 7, figs. 37, 38; Pl. 8, figs. 47–50; Pl. 9, figs. 63, 64; Pl. 12, fig. 74; Text-figs. 44–49)

DIAGNOSIS. Larger shoots 10 mm. in diameter, branching at an acute angle in one or more planes to give off branchlets typically 2 mm. in diameter. Leaves spirally attached to rhomboidal or somewhat oval leaf base cushion, large leaf with cushion typically 7.5 mm. long \times 3.5 mm. broad; normal size 3–4 mm. long \times 1.5–1.75 mm. broad; length usually about twice breadth. Free part of leaves (upper side) $\frac{1}{3}$ to $\frac{1}{4}$ of total length. Leaves with rounded or acute apex. Venation not seen. Thickness of lamina up to 0.8 mm. measured in laterally compressed specimens.

Cuticle thick, up to 3 μ , lower slightly thicker than upper. Margins of leaves entire with distinct projection of marginal cells, transversely elongated, up to 100 μ long, appearing serrate where both cuticles join. Stomata present on both cuticles, numerous, tending to form longitudinal rows, particularly in central part of lamina. Stomata usually absent near apices of leaves on lower cuticle, and present near margins and base. Stomata on both cuticles variably orientated; in some rows tending to be transverse. Stomata of a row often with subsidiary cells in contact, but usually separated by one or more epidermal cells. Stomata rarely sharing a subsidiary cell. Stomatal rows separated by 2–4 rows of square or rectangular epidermal cells.

Epidermal cells located on same rows as stomata, usually isodiametric, occasionally transversely elongated, typically 20–25 μ . Epidermal cells between rows of stomata usually square or rectangular, 20–30 μ , rarely elongated up to 100 μ . Epidermal cells on margins and apex square or rectangular. Epidermal cells on base typically isodiametric. Periclinal cell walls straight, unpitted, with distinct border, up to 5–7 μ broad (including two borders and middle lamella). Anticlinal walls cutinized. Cell surface generally flat with round or elongated irregular granules, sometimes forming compact ring near border of walls. Striae and ridges present, sometimes anastomosing to form a reticulum.

Stomata similar on both cuticles, typically monocyclic, rarely imperfectly dicyclic. Stomatal apparatus usually oval but occasionally circular. Guard cells slightly sunken in oval or round pit, feebly cutinized, 40–50 μ long \times 30 μ wide (both)



Brachyphyllum brettii sp. n.

- FIG. 44. General aspect of the holotype, showing branching. LIL 2565. $\times 2$.
 FIG. 45. Small leaf. Slide V.44671. $\times 15$.
 FIG. 46. Section of stoma. $\times 500$.
 FIG. 47. Leaf of a normal size. V.44673. $\times 15$.
 FIG. 48. Stoma showing sunken guard cells (broken lines) and a few striae on subsidiary cells. Slide LIL 196. $\times 500$.
 FIG. 49. Stoma showing numerous striae on subsidiary cells. Slide LIL 194. $\times 500$.

surrounded by typically 4-5 subsidiary cells. Polar and lateral subsidiary cells usually not differentiated. When two cycles of subsidiary cells are present, the inner cells are narrow and curved following the edge of mouth of pit. Encircling cells larger. Mouth of pit marked by more or less continuous rim of cutin, formed by fusion of subsidiary cells. Occasionally, subsidiary cells with 1 or 2 ridges parallel to mouth of pit.

Hypodermal cells sometimes cutinized, markedly elongated.

HOLOTYPE. LIL PB n. 2565.

MATERIAL. In addition to the holotype, LIL PB 2570(a), 2567(a), 2571-72, 2575(a); Brit. Mus. (Nat. Hist.) nos. V.44670, V.44676. Slides: LIL 185-199; V.44671-75.

DESCRIPTION. This species is common in the *Ticoa harrisii* bed. One specimen has a large branch, 1 cm. wide, with leaves still attached. The leaves are more or less separated.

Some of the shoots definitely branch in more than one plane. The cuticle is very well preserved and easy to prepare. The lower cuticle is thicker than the upper, which stains more strongly with safranin. The natural colour of the cuticle is brown.

The lamina substance (mesophyll) is often carbonized. These fragments when treated with dilute ammonia rapidly dissolve leaving no definite trace of tissues.

On the lower cuticle there is sometimes a longitudinal median area, about 10 cells wide, devoid of stomata. The stomatal pits are clearly seen, but the guard cells are sometimes absent. The hypodermal cells are very seldom visible.

The branchlets of *Brachyphyllum brettii* are given off at a more acute angle than those of *B. mucronatum*. The ratio of length and breadth of the leaves in these two species, as well as the natural colour of the cuticle is also different. The marginal cells of the leaves forming serrate projections are more obvious in *B. brettii* and are present on the apical part of the leaf. This character, shared by all the Ticó specimens, is met with in some Northern specimens of related genera such as *Pagiophyllum magnipapillare* Wesley (1956, text-fig. 18, G) and *Cheirolepis muensteri* Schenk (Lewarne & Pallot, 1957, text-fig. 2, B). The epidermal cells in *B. brettii* tend to be isodiametric, while in *B. mucronatum* they are usually rectangular, especially between rows of stomata. The cell surface is much more sculptured than in *B. mucronatum*, resembling in this respect the sculpturing in *B. mirandai*. *B. brettii* differs from *B. mirandai* in the length of the free part of the leaf (upper cuticle) and in the thickness of the lamina substance (mesophyll). In *B. mirandai* the epidermal cells are usually larger, the periclinal cell walls are much thicker and the hypodermal cells are much more strongly cutinized than in *B. brettii*. For comparison with species from other countries, see p. 76.

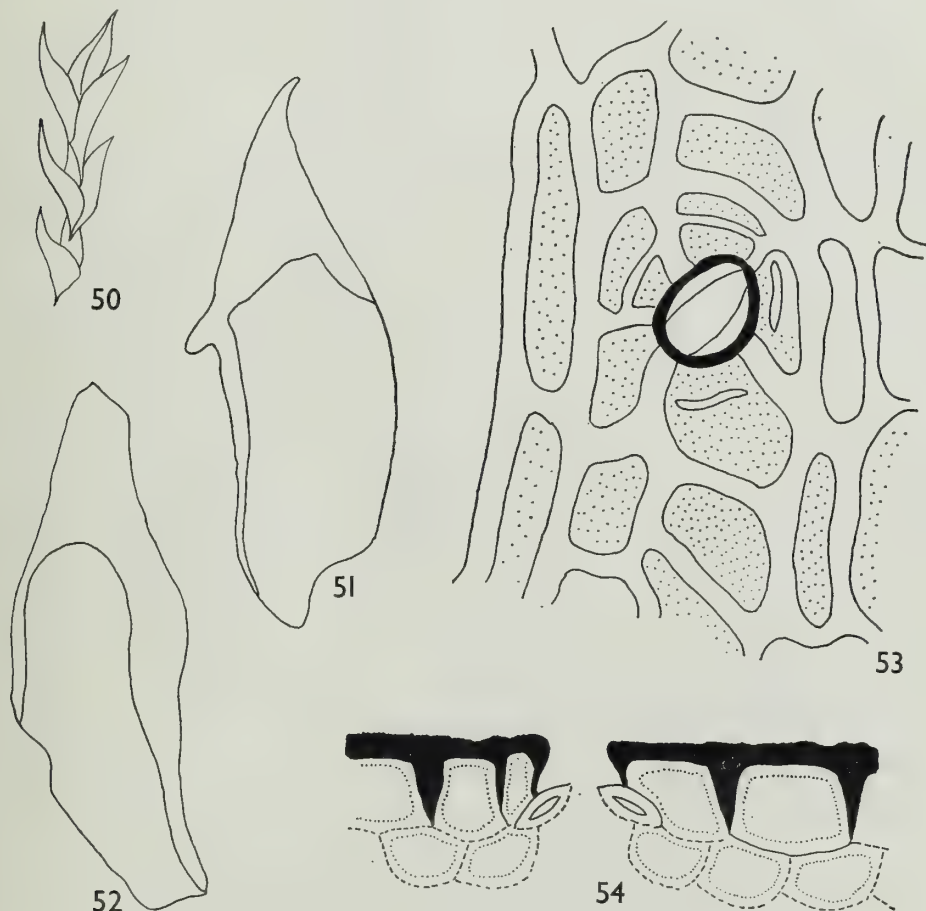
The species has been named after Donald W. Brett, Botany Department, The University, Glasgow.

Brachyphyllum mucronatum sp. n.

(Pl. 7, fig. 43; Pl. 8, figs. 51, 52; Pl. 10, fig. 66; Pl. 12, fig. 75; Text-figs. 50-54)

DIAGNOSIS. Largest branch known 3 mm. in diameter, giving off lateral branch-

lets, 1.5 mm. diameter, at an acute angle of approximately 45° . Branching in one or more planes. Leaves attached spirally to oval leaf base cushion, largest known 5 mm. long \times 1.5–1.7 mm. broad. Ratio between breadth and length 1 : 2, 3–1 : 3.



Brachyphyllum mucronatum sp. n.

FIG. 50. Fragmentary branchlet showing a few spirally attached leaves. V.44670. $\times 4$.

FIGS. 51, 52. Leaves of normal size. Slides LIL 200, 201. $\times 15$.

FIG. 53. Stoma showing two ridges on subsidiary cells. Slide LIL 201. $\times 500$.

FIG. 54. Section of stoma. $\times 500$.

Free part of leaves typically $\frac{1}{3}$ of total length. Leaves usually with acute apex, often projecting towards branch axis and mucronate. Venation not seen.

Cuticle thick. Apical part of leaves with sharp margin formed by layer of transversely projecting cells up to 50μ long, edge microscopically serrate. Stomata occurring on both sides of lamina and on cushions; on adaxial side of leaf generally

distributed, on abaxial side distributed over basal cushions and margins but usually absent near leaf apex. Stomata forming short rows, rows ill-defined but more definite near midline of lamina, stomatal orientation varied, but frequently longitudinal. Stomata of a row sometimes with subsidiary cells in contact but usually separated by one or more epidermal cells. Stomata very rarely sharing a subsidiary cell. Stomatal rows typically separated by 2–4 files of rectangular elongated epidermal cells.

Epidermal cells located on same rows as stomata, usually isodiametric, $25\text{--}40\ \mu$, sometimes transversely elongated. Epidermal cells between stomatal rows typically rectangular, $60\text{--}70\ \mu$ long \times $10\text{--}15\ \mu$ broad, rarely up to $100\ \mu$ long. Epidermal cells at base typically isodiametric, sometimes bearing a single round papilla. Epidermal cells on margins rectangular or slightly elongated. Epidermal cells near apex rectangular, tending to be isodiametric near apical margin. On upper cuticle, epidermal cells rectangular or isodiametric. Periclinal walls straight, unpitted, with distinct border, up to $5\text{--}6\ \mu$ broad (including 2 borders and middle lamella). Anticlinal walls cutinized. Cell surface flat. Delicate striae parallel to border of cells. Basal cells often with delicate granules, rarely conspicuous ones.

Stomata similar on both cuticles, typically monocyclic, sometimes imperfectly dicyclic. Stomatal apparatus usually oval but occasionally circular. Guard cells slightly sunken in oval or round pit, feebly cutinized, about $50\ \mu$ long, surrounded by typically 4–5 subsidiary cells. Polar and lateral subsidiary cells usually not differentiated, sometimes with anticlinal walls extending to hypodermis. Mouth of pit marked by more or less continuous rim of cutin, formed by fusion of subsidiary cells. Subsidiary cells usually with a ridge parallel to mouth of pit, ridges sometimes united to form a ring.

Hypodermal cells sometimes feebly cutinized, markedly elongated.

HOLOTYPE. LIL PB n. 2569.

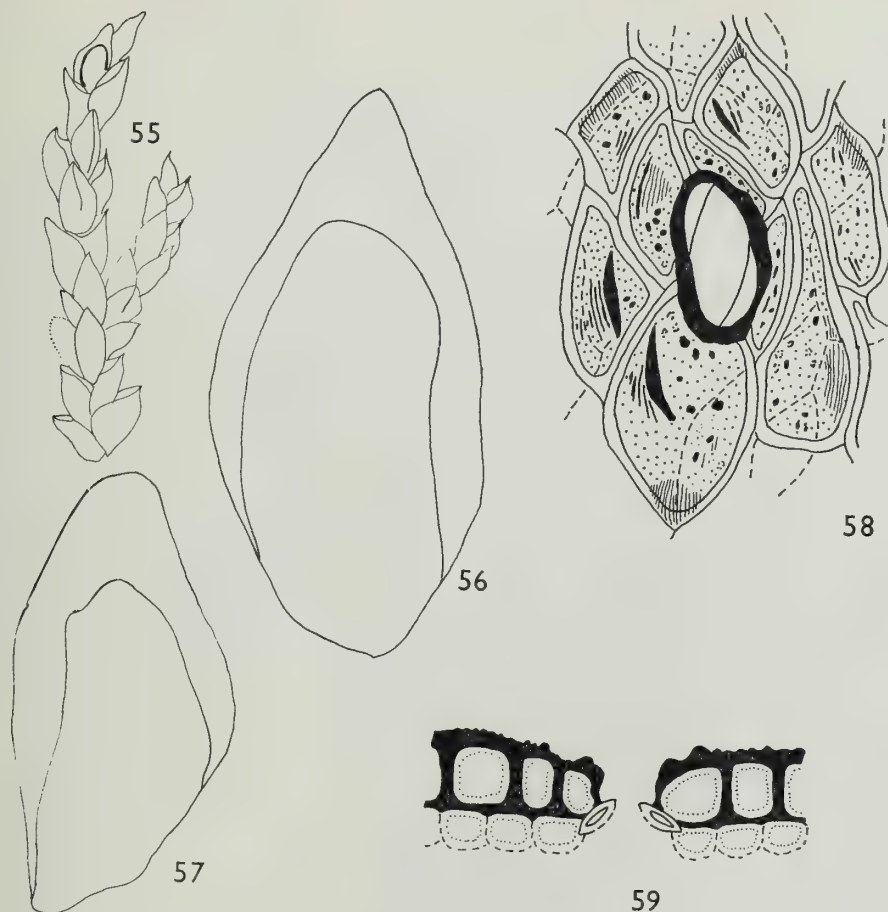
MATERIAL. In addition to the holotype LIL PB n. 2573; Brit. Mus. (Nat. Hist.) no. V.44670. Slides: LIL 200–214; V.44669.

DESCRIPTION. This species is present in the *Ticoa harrisii* bed, and is as abundant as *Brachyphyllum brettii*. Branchlets of *B. mucronatum* are often found mixed with twigs of *B. brettii*. They can be distinguished macroscopically by the lighter colour of the cuticle of *B. mucronatum* (yellowish-brown) and by their leaves which are more acute, but the two species can only be separated with certainty by the microscopical characters of their cuticles.

Brachyphyllum mucronatum differs from *B. mirandai* as follows:

In *B. mucronatum* the leaf is relatively narrower (1.5 mm. as against 4 mm.) and the free part of the leaf is a longer portion of the whole ($\frac{1}{3}$ as against $\frac{1}{4}$). The cuticle is paler, thinner and less prominently sculptured than in *B. mirandai* and its hypodermal cells are less cutinized. The apex of the leaf is more acute in *B. mucronatum* than in *B. mirandai* or indeed in any other species described here, and there is a tendency for it to curve further inwards towards the branch axis.

The narrowness of the leaves of *B. mucronatum* may be compared with some Northern species of *Pagiophyllum* but the free part of the leaf is always much shorter than the length of the leaf base cushion.



Brachyphyllum mirandai sp. n.

FIG. 55. Fragment of the holotype showing branching. LIL 2560. $\times 2$.

FIGS. 56, 57. Normal and small leaves. Slide LIL 215. $\times 15$.

FIG. 58. Stoma showing abundant granules, striae and ridges on subsidiary cells. (Hypodermal cells with broken lines). Slide LIL 216. $\times 500$.

FIG. 59. Section of stoma. $\times 500$.

Brachyphyllum mirandai sp. n.

(Pl. 7, fig. 41; Pl. 8, figs. 53-55; Pl. 9, figs. 61, 62; Pl. 12, fig. 76; Text-figs. 55-59)

DIAGNOSIS. Larger branch, 4 mm. in diameter, giving off smaller lateral branchlets at acute angle. Leaves spirally attached to rhomboidal or rounded leaf base cushion; largest leaves 7 mm. long \times 4 mm. broad; normal size 4-5 mm. long \times 2-2.5 mm. broad. Free part of leaf about $\frac{1}{4}$ of total length. Apex rounded or acute. Sub-

stance of lamina up to 1.2 mm. thick, measured in laterally compressed leaves. Venation not seen. Median keel sometimes seen on abaxial surface of leaves.

Cuticle thick. Sharp margins formed by layer of transversely projecting cells up to $70\ \mu$ long, edge microscopically serrate. Stomata numerous, present on both sides of free part of leaves and on leaf cushion, usually absent near apex. Stomata normally scattered but sometimes forming short ill-defined longitudinal rows. Stomata usually orientated longitudinally, often obliquely, rarely transversely; lateral subsidiary cells of neighbouring stomata in contact; rarely two stomata sharing a lateral subsidiary cell.

Epidermal cells usually slightly elongated, rectangular, polygonal, sometimes square. Rectangular cells typically $80\text{--}100\ \mu$ long \times $35\text{--}45\ \mu$ broad. Typical isodiametric cells on lamina and margins about $50\ \mu$ in diameter. Periclinal walls straight, about $10\ \mu$ thick, rarely pitted, with a distinct border. Anticlinal walls cutinized down to hypodermis. Surface flat with irregularly distributed striae, granules or occasional reticulations. Occasionally one or more very small papillae present near marginal cells.

Stomata similar on both cuticles, typically monocyclic or imperfectly dicyclic. Guard cells typically $60\ \mu$ long \times $40\ \mu$ wide (when open) sunken in oval or round pit, feebly cutinized, surrounded by typically 4–5 subsidiary cells, not well differentiated into polar and lateral. Mouth of pit sometimes marked by rim of cutin formed by fusion of borders of subsidiary cells. Subsidiary cells with usually one, sometimes two strong ridges parallel to mouth of pit. Numerous distinct striae and granules of varying size present on subsidiary cells. Encircling cells, when present, also with ridges, numerous striae and granules.

Hypodermal cells cutinized on same level as guard cells, markedly elongate.

HOLOTYPE. LIL PB n. 2560.

MATERIAL. In addition to the holotype, LIL PB n. 2559, 2561; Brit. Mus. (Nat. Hist.) no. V.44668. Slides: LIL 215–217.

DESCRIPTION. This conifer was found in a new bed in which it is the dominant element. The matrix of the rock is thin, much more compact than in the *Ticoa harrisii* bed, and darker (brown) in colour. The cuticles also look much darker.

The branching of the specimens is imperfectly known, the material being too fragmentary. However, in a few specimens that show branching it seems to be in more than one plane.

The stomatal apparatus usually stains more strongly with safranin than the rest of the epidermis and it can be clearly seen that the strongly sculptured outer (periclinal) walls of the subsidiary and encircling cells obscure the vertical (anticlinal) walls of these cells.

DISCUSSION. *Brachyphyllum mirandai* is distinguished from all other species of *Brachyphyllum* more readily than *B. breittii* because of the unique surface sculpture of its subsidiary cells. However, *Pagiophyllum peregrinum* (L. & H.) from the Lower Lias of Lyme Regis, Dorset has rather similar striae (Kendall, 1948: 83) but no granules or reticulations. Furthermore the stomata of *P. peregrinum* are arranged in longitudinal rows and are usually transversely orientated, features which do not occur in *B. mirandai*. The encircling cells of the European species seem to

form a more constantly differentiated ring than in *B. mirandai*. The epidermal cells of *P. peregrinum* are smaller and trichomes have been observed. The cell walls, however, are sometimes pitted as in *B. mirandai*. Finally, twigs of *P. peregrinum* are usually broader than those of *B. mirandai*.

A cuticle has been described by Hörhammer (1933) from vegetative shoots of *Cheirolepis muensteri* Schenk which resembles in every respect the cuticle of *Brachyphyllum*. The leaves figured by him (1933, pl. 1, figs. 9, 9a, 9b) have somewhat dentate margins and a markedly acute apex. The stomata are arranged in definite longitudinal rows and the epidermis appears to be granulated. The subsidiary cells of the stomata in *C. muensteri* are more markedly striated and the cells between the stomatal rows are more elongated than in *B. mirandai*.

Lewarne & Pallot (1957) describe *C. muensteri* from the Rhaeto-Liassic of South Wales. The leaves are generally smaller than those of *B. mirandai*, but the shape is similar. The adaxial cuticle is much smaller in relation to the abaxial one, than in *B. mirandai* but the subsidiary cells of the stomata have a rather prominent ridge running parallel with the pit which is similar to that described in all our species of *Brachyphyllum*. Furthermore, the leaf margins, especially near the apex, are specialized, with a distinct cuticular projection as shown in Text-fig. 2, B. This is also comparable with our species.

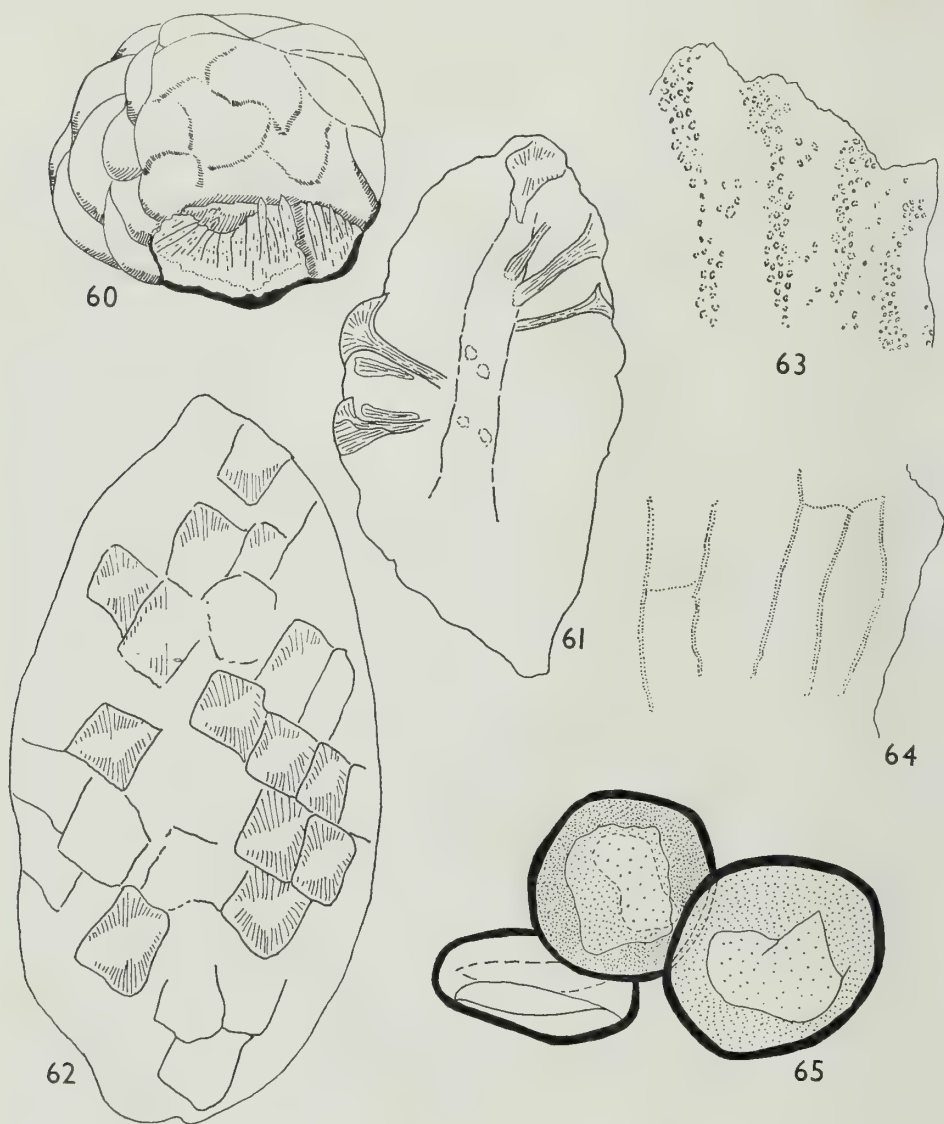
The species is named after Mr. H. Miranda who was the first to discover the plant bed with cutinized specimens in the Ticó Amphitheatre in 1957.

Male cones associated with *Brachyphyllum mirandai* sp. n.

(Pl. 7, figs. 45, 46 ; Text-figs. 60-65)

Several small cones were found in the bed containing the sterile twigs of *B. mirandai*. Some are compressed vertically and others longitudinally. None of them has a stalk (LIL PB 2561-62). The shape of these cones is elliptical. One specimen, compressed vertically, has a width of 4 mm. Impressions of the heads of the microsporophylls are clearly seen and they are more or less rhomboidal in shape. In one corner, a thick layer of strongly compressed tissue was found. After maceration this tissue proved to be composed of compressed cuticles of microsporophylls with their pollen sacs ; all details of their original shape have been obliterated. The pollen sacs could be seen on the actual specimen projecting inwards as sharp teeth, but it is not possible to determine their number. The cuticles are unsatisfactorily preserved but two kinds were noted. One, possibly belonging to the microsporophyll or the outside of the pollen sac, shows dark elongated cells 10 μ wide and is not granular. The other, the lining of the pollen sac, also shows elongated cells 10 μ wide but is covered with prominent granules, typically 1-2 μ wide. These granules are detachable and also adhere to the pollen grains.

Another cone, longitudinally compressed, measures 8 mm. long \times 4 mm. wide. The median axis is seen, its width being about 0.8 mm. Round scars, corresponding to the insertion of vertically compressed microsporophylls, can be seen arranged in a spiral on the main axis of the cone. The microsporophylls are about 1.5 mm. long and are inserted at right angles or slightly obliquely to the main axis. The stalk is straight and at the end expands in a wide head which is transversely elongated to the



Male cone associated with *Brachyphyllum mirandai* sp. n.

FIG. 60. Vertical compression showing some pollen sacs. LIL 2561. $\times 10$.

FIG. 61. Lateral compression showing some stalks and heads of microsporophylls still attached to the cone axis. LIL 2562. $\times 10$.

FIG. 62. Lateral compression showing rhomboidal heads of sporophylls. LIL 2562. $\times 10$.

FIG. 63. Granulose membrane. Slide LIL 224. $\times 500$.

FIG. 64. Smooth membrane showing cellular outlines. Slide LIL 224. $\times 500$.

FIG. 65. Pollen grains. Slide LIL 221. $\times 500$.

stalk of the microsporophylls. Two (or more?) pollen sacs are attached in the inner part of the head and extend towards the main axis of the cone. The pollen sacs are long, somewhat fusiform and have longitudinal striations. After macerating the microsporophylls of this cone the same two types of cutinized membranes were seen, one with dark elongated cells and the other, thinner, with prominent granules. The pollen is rare but similar to that found in the previous cone. No other type of pollen was seen.

A third specimen, also a longitudinally compressed male cone, is oval in shape and measures 1 cm. in length and 0.5 cm. in breadth. Although the innermost part of the cone has disappeared, the external prints of the heads of the microsporophylls are clearly seen. They are perfectly rhomboidal and arranged in a spiral. Each head measures about 1 mm. \times 1 mm. Fine striations are given off from the central part of the heads.

A constant feature of these cones is that they are always found without stalk or sterile foliage at their base.

Pollen. The pollen grains are alike in the two cones which have been macerated. The sporangia have dehisced and shed nearly all their pollen, but a few grains, all of one type, remain on the granulose membrane. Most of the pollen grains are circular, 50–55 μ wide, with an exine 3 μ thick. There are no wings. The surface is almost smooth but may be very faintly granular. Most grains show some irregularly orientated folds which are probably due to compression. Other folds are usually arranged in a circular manner, surrounding a middle pale area which is here presumed to be the sulcus. These circular folds may be the original edges of the sulcus which was concave. A few of the grains are oval and these are regarded as having been laterally compressed; their folds are entirely consistent with the idea that the pale area is a sulcus. The grains thus, may have been flattened discs with one concave side.

One grain shows a separate round body, 30 μ wide, with a well-developed wall. This body is present on the other side of the disc and could have been another concave or flat circular area. This feature has not been seen in any of the other specimens, and its nature is unknown.

The combined data available from these cones give a fairly complete picture of their structure. Unfortunately the important information regarding the number and position of pollen sacs is lacking. The definition of these male cones is as follows:

Male cones elliptical, found always detached from the shoots, without stalk, typically 8–10 mm. long \times 4–5 mm. wide. Microsporophylls arranged spirally, inserted to one main central axis about 0.8 mm. wide, in a perpendicular or slightly oblique manner. Heads of sporophylls typically rhomboidal, crowded, forming a close structure. Two cuticles are seen. One, probably of the microsporophyll, is thick, with dark elongated cells about 10 μ wide. The other, thinner, also with elongated cells about 10 μ wide, is crowded with prominent granules typically 1–2 μ wide. Pollen sacs elongated. Pollen grains (when compressed) circular and flattened, typically 50–55 μ wide. Exine 3 μ thick. No wings present, surface smooth. A middle thinner area is seen, probably corresponding to the sulcus.

DISCUSSION. These three male cones are considered to belong to the same species, because they are found in the same bed, they are approximately the same size and their pollen and cutinized membranes are similar. They may belong to the same plant as the foliage *Brachyphyllum mirandai* sp. n. which so far is the only conifer foliage that has been found in the same bed.

This type of cone and the pollen it bears is different from all Taxopsida and from most of the Pinaceae, Cupressaceae and Podocarpaceae. Similar cones are found in the Araucariaceae and Taxodiaceae, mainly in the genera *Araucaria*, *Agathis*, *Cryptomeria* and *Sciadopitys*. If we accept the evidence of their close association as an indication that the cones and foliage belong to the same plant, *B. mirandai* may then be compared closely with the Araucariaceae; but this has still to be proved.

The pollen grains of *Cheirolepis muensteri*, although similar in shape, are smaller than those described above ($20-30\ \mu$), and have a thickened exine in the equatorial region. There is a similarity in shape with pollen grains of *Classopollis torosus* (Reissinger) type and the range in size coincides with our material (up to $46\ \mu$). Couper (1958) believes that *C. torosus* grains are similar to those found in male cones of *Pagiophyllum connivens*. However, I could not see the characteristic equatorial thickenings of *C. torosus* in our pollen. Couper points out that none of the Recent conifers possesses pollen of this type.

Harris (1957) described carbonized fragments of *C. muensteri* from Wales. The fragments of male cones yielded supplementary information about the nature of the microsporophylls which are inserted spirally on the main axis, as in the Ticó specimens, but the heads of the sporophylls seem to be larger. The number of microsporophylls in the cones was probably smaller in *Cheirolepis* than in the Patagonian specimens. Unfortunately it has not been possible to compare the number and size of the pollen sacs owing to the fragmentary nature of our material. The shape of the pollen grains of the Welsh material is similar, but the grains are smaller and the tuberculate equatorial area figured by Harris (1957, text-fig. 5, A-C) is not evident in the Patagonian specimens.

The compressed material described by Hörhammer (1933, pl. 4, figs. 27, 27A) looks rather different from our specimens.

Some male cones found in association with *Brachyphyllum* and *Pagiophyllum* can be compared with the present specimens. Kendall (1952) described male cones associated with *Pagiophyllum connivens* from the Jurassic of Yorkshire. They are wider than the Patagonian cones, having a diameter of 7 mm. The pollen grains are much smaller ($20-30\ \mu$) but the exine has the same thickness. Other microstrobili have been found attached to *Brachyphyllum mamillare* and have been described by Kendall (1949). The diameter of these cones is somewhat smaller than the previous species mentioned, and are thus more comparable to ours. The pollen grains have more or less the same size and have no marked sculpturing on the exine.

I can make no comparison with the presumed male cones found associated with *Athrotaxis ungeri* (Halle, 1913, pl. 3, fig. 21) described from the Upper Mesozoic

strata of Río de los Fósiles, Argentina. The cone is longitudinally compressed and has lost all traces of organic matter; there is no information about the cuticles or pollen grains.

Brachyphyllum irregulare sp. n.

(Pl. 7, fig. 44; Pl. 8, figs. 56, 57; Pl. 10, fig. 65; Pl. 12, fig. 77; Text-figs. 66-71)

DIAGNOSIS. Largest branches known, 2 mm. in diameter, giving off lateral branchlets, about 1 mm. in diameter, at an acute angle. Leaves spirally attached to an oval leaf base cushion on branchlets typically 3 mm. long \times 2 mm. wide with rounded apex. Leaves on largest branches up to 6 mm. long \times 3 mm. wide, usually with acute apex. Free part of leaves typically $\frac{1}{3}$ of total length. Ratio between length and breadth 1.5 : 1-2 : 1. Venation not seen.

Cuticle thick. Sharp margins formed by layer of transversely projecting cells up to 80 μ long, edge microscopically serrate. Stomata present on both cuticles and leaf cushion but becoming less numerous near leaf apex, on both sides. Stomata placed irregularly, typically not forming rows, rarely forming short, ill-defined rows of not more than 3-4 stomata long; orientation varied but with slight tendency to be longitudinal. Stomata sometimes with subsidiary cells in contact, rarely sharing one.

Epidermal cells usually isodiametric, 35-50 μ , often somewhat rectangular, longitudinally elongated, rarely up to 100 μ long. Epidermal cells on both cuticles similar on margins, base, apex and lamina. Periclinal walls straight, sometimes pitted, with distinct border, up to 5-7 μ wide (including 2 borders and middle lamella). Anticlinal walls cutinized. Cell surface flat, very finely granular.

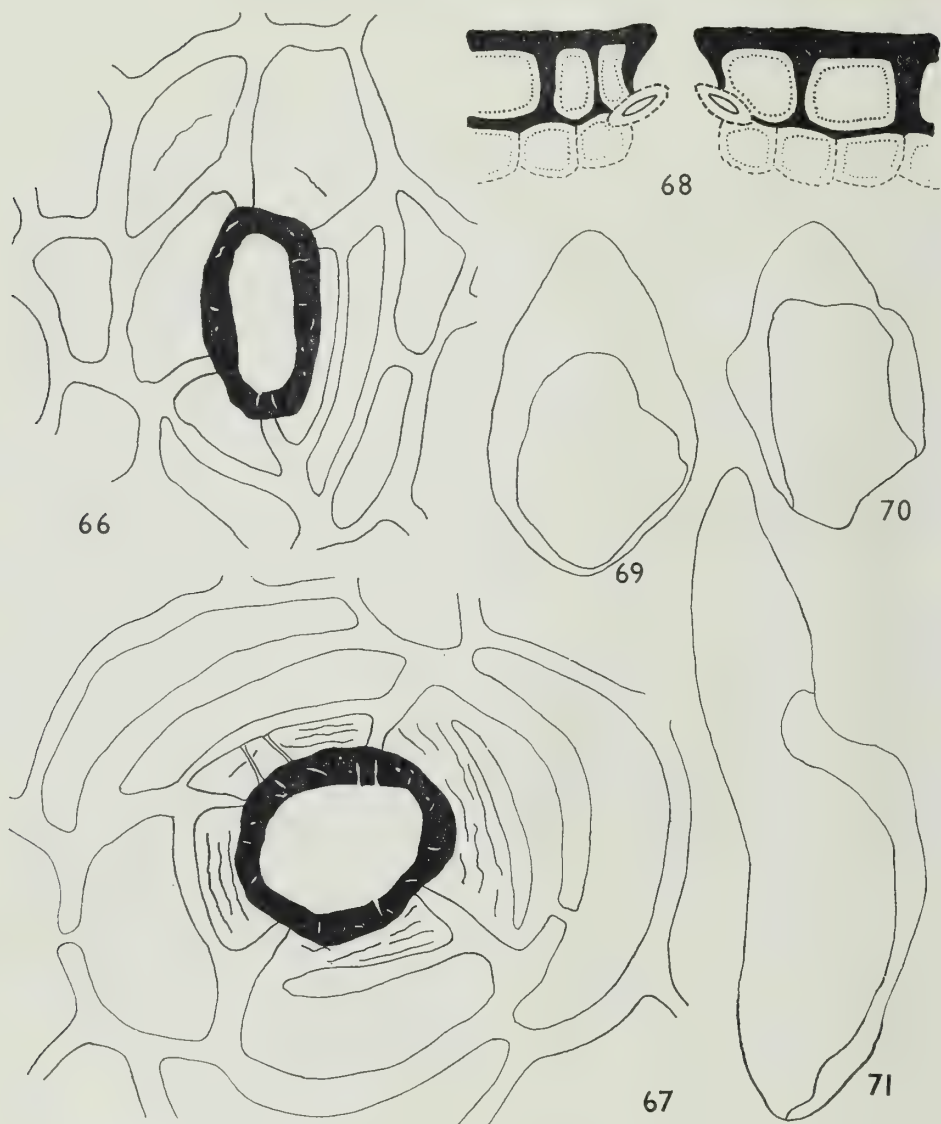
Stomata similar on both cuticles, typically monocyclic or imperfectly dicyclic. Dicyclic stomata sometimes seen on upper cuticle. Stomatal apparatus usually oval but sometimes circular. Guard cells not cutinized, surrounded by typically 4-5 subsidiary cells. Polar and lateral subsidiary cells usually not differentiated. Mouth of pit marked by more or less continuous rim of cutin which stains less strongly with safranin and has irregular striae. Subsidiary cells usually with ridge parallel to mouth of pit. Ridges of adjacent cells sometimes united to form a ring. Rarely, on surface of subsidiary cells there are perpendicular ridges to mouth of pit. Pitting in anticlinal walls of subsidiary cells to stomatal pit.

Hypodermal cells cutinized, narrow and markedly elongate.

HOLOTYPE. LIL PB n. 2576.

MATERIAL. In addition to the holotype, LIL PB n. 2577-79, 2582; Brit. Mus. (Nat. Hist.) no. V.44667. Slides: LIL 255, 233.

DESCRIPTION. *Brachyphyllum irregulare* was found in a new bed where it is abundant with *Cladophlebis*. Its cuticle is brown in colour. The rim of cutin surrounding the mouth of pit stains less strongly with safranin than does the rest of the cuticle and hence appears light in colour. The numerous pits which appear to traverse the anticlinal walls of the subsidiary cells bordering the stomatal pit are a constant feature.



Brachyphyllum irregulare sp. n.

FIG. 66. Stoma on lower cuticle. Slide LIL 225. $\times 500$.

FIG. 67. Stoma on upper cuticle showing some striae and ridges. Slide LIL 225. $\times 500$.

FIG. 68. Section of stoma. $\times 500$.

FIGS. 69, 70. Two leaves of normal size. Slide LIL 225. $\times 15$.

FIG. 71. A large leaf. Slide LIL 233. $\times 15$.

This species differs from all others of *Brachyphyllum* described in the present paper in the irregular distribution of stomata which do not form rows. The periclinal walls are pitted, as in *B. mirandai*, but the cell surface sculpturing is less conspicuous.

B. crucis Kendall from the Middle Jurassic of Yorkshire and Wiltshire is similar in that the stomata do not form definite rows. Its stomata are different, however, in having bulging subsidiary cells and hypodermal cells that are nearly isodiametric. In fact, *B. crucis* differs from typical *Brachyphyllum* species in the absence of definite longitudinal rows of stomata as does *B. irregulare*. In this respect, these two species are unlike any known Araucariaceae, living or fossil, but they resemble some Podocarpaceae such as *Podocarpus ustus* (Florin, 1933 : 270). Leaving our species in *Brachyphyllum* (an unnatural genus) I should stress the diagnostic feature of the stomata which usually tend to form, but sometimes do not form longitudinal rows. With this emendation the Patagonian species may be included in the genus *Brachyphyllum*.

Brachyphyllum expansum var. *indica* Sahní (1928) has a similar stomatal arrangement (not forming rows). The leaves are smaller, however, and there is no information about the stomata to make a clear comparison.

Athrotaxis ungeri (Halle)

(Pl. 6, fig. 35 ; Pl. 7, fig. 42 ; Pl. 10, figs. 67-69 ; Pl. 12, fig. 78 ; Text-figs. 75-79)

EMENDED DIAGNOSIS. Twigs branched. Largest branches 2-3 mm. wide. Branchlets given off at acute angle. Leaves spirally attached to rhomboidal leaf base cushion. Leaves small with acute apex and broad base, typically 2 mm. long \times 1.5 mm. broad. Free part of leaves (upper side) $\frac{1}{2}$ to $\frac{1}{3}$ of total length. Margins slightly dentate. Venation not seen. Leaves not spreading out but markedly adpressed to shoot, with apical part sometimes curved towards branch.

Lower cuticle, 7 μ thick, much thicker than upper cuticle. Stomata present on upper cuticle, very rarely at base of lower cuticle. Stomata not forming rows, variably orientated.

Epidermal cells on lower cuticle typically square or isodiametric, 30-40 μ wide, or rectangular, elongated, 50 μ long \times 20-25 μ wide, becoming markedly elongate towards margins. Cells forming definite longitudinal rows, one cell wide. Leaf margins marked by cells 60 μ long \times 20 μ wide which project outwards almost perpendicularly, with their apices free, as teeth. Anticlinal cell walls straight, cutinized down to hypodermis, sometimes pitted. Periclinal cell walls smooth, except for base of leaf where they are finely granulose with strongly marked round or slightly elongated single pinnae on almost every cell. Hypodermal cells cutinized, markedly elongated, much narrower than epidermal cells.

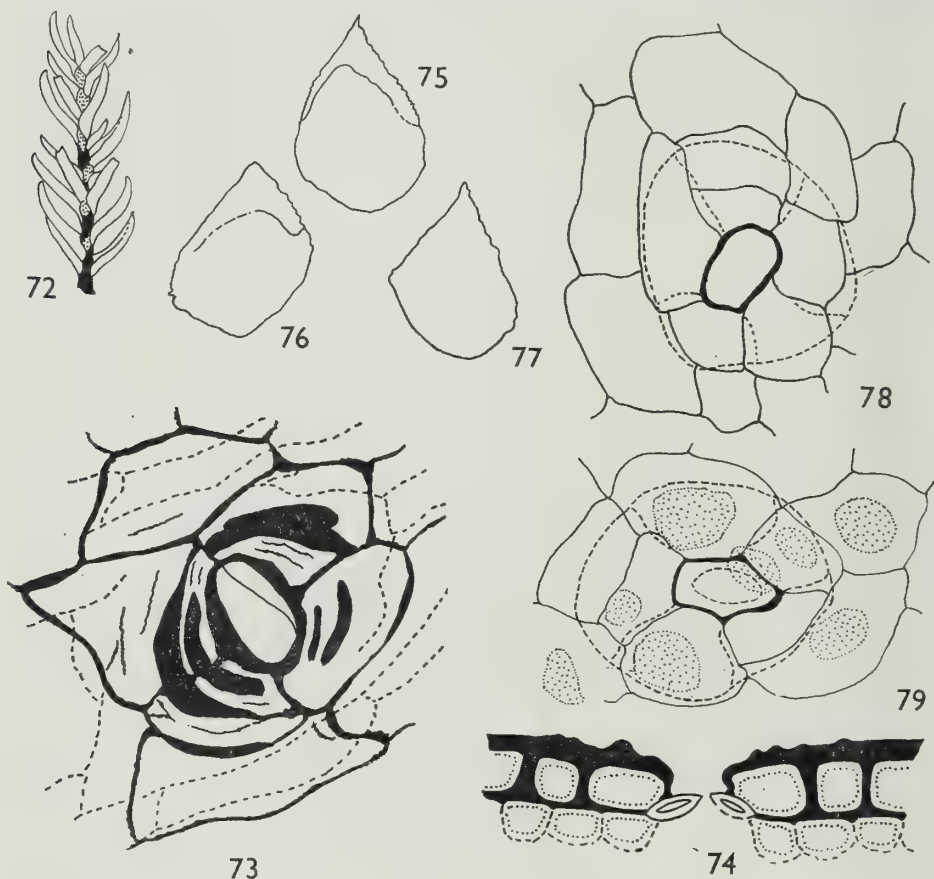
Epidermal cells on upper cuticle typically isodiametric with somewhat rounded contours, about 30-40 μ wide. Anticlinal cell walls not so strongly marked as on lower cuticle, straight, sometimes pitted. Periclinal cell walls finely granulose.

Stomata typically monocyclic, sometimes imperfectly dicyclic. Mouth of pit oval or sometimes polygonal, surrounded by typically 5 subsidiary cells. Guard cells sunken in pit, producing an oval or circular outline, underneath outer cuticle

of subsidiary cells. Stomata on base of lower epidermis of leaves with subsidiary cells bearing strong round papillae, sometimes projecting over mouth of pit.

MATERIAL. LIL PB n. 2563. Slides: LIL 226-228; Brit. Mus. (Nat. Hist.) nos. V.44662-63.

DESCRIPTION. This species was found in a new bed where Bennettitalean fronds are abundant. The branches are few, grouped together and perhaps belonging to a



Tomaxellia d. giustoi gen. et sp. n.

FIG. 72. Holotype. LIL 2542 (b). $\times 2$.

FIG. 73. Stoma showing strong ridges on subsidiary cells and cutinized hypodermal cells (broken lines). Slide LIL 229. $\times 500$.

FIG. 74. Section of stoma. $\times 500$.

Athrotaxis ungeri (Halle)

FIGS. 75-77. Leaves of normal size. V. 44662. $\times 15$.

FIGS. 78. Stoma on upper cuticle. Slide LIL 228. $\times 500$.

FIG. 79. Stoma on basal part of lower cuticle. Slide LIL 226. $\times 500$.

single tree; they are all fragmentary. The small leaves are markedly adpressed to the branches and their lower sides, almost devoid of stomata, must have been facing the sun.

The cuticle is very well preserved although the adaxial, because it is thin, is difficult to prepare. The abaxial cuticle consists of two distinct areas, the proximal being the third nearest the axis and the distal the remaining two-thirds. The proximal part is formed by cells with granular surface and bearing strong papillae, but the distal part shows cells with a smooth surface and no papillae at all. The adaxial cuticle shows no such division into areas, the outline of the cells being rounded. The margins of the whole leaf show tooth-like projections. The stomata on both cuticles are alike in structure and size, but those on the abaxial cuticle always have strong papillae on the subsidiary cells.

DISCUSSION. *Athrotaxis ungeri* differs from all other conifers described in this paper. It resembles *Brachyphyllum* in the shape of its leaves and in their spiral arrangement on the branch, but the leaves differ in size and the cuticular structure is quite different. This species cannot be included in the genus *Brachyphyllum* as modified by Kendall (1947), because the stomata never form rows and are almost completely absent from the abaxial cuticle.

A. ungeri can be compared with the living *Athrotaxis*. The leaves are the same shape and size as those of *A. cupressoides*, but they differ from the other two species of this genus. In this species, as in ours, the leaves are closely adpressed to the branches. The cuticular structure of *A. cupressoides* also has some similarities with that of *A. ungeri*: the lower cuticle is thicker than the upper and the epidermal cells are similar in shape. Furthermore, in the basal part of the leaf, each cell bears a single strongly marked papilla. The stomata never form longitudinal rows in either species and neither species has stomata on the abaxial sides of the distal $\frac{2}{3}$ of the leaf. The only difference between them is that while there are just a few stomata on the abaxial side of the proximal $\frac{1}{3}$ of the leaf in *A. ungeri*, there are a good many in *A. cupressoides*. The stomata of the two species appear to be very similar.

Many other conifers (*Juniperus chinensis*, *Cupressus sempervirens*, *Diselma archeri*, *Microbiota decussata* and *Chamaecyparis pisifera*) have a similar stomatal arrangement (few on the lower cuticle, mainly near the base). They all belong to the Cupressaceae which have a different leaf arrangement from that of *A. ungeri* (opposite, not spiral) and their stomatal apparatus is also rather different. *Microcachrys tetragona* (Podocarpaceae) should also be mentioned as having a similar arrangement of stomata but with a different leaf arrangement, stomatal apparatus and shape of epidermal cells.

Thus although various Recent conifers match the fossil in certain respects they differ in others, and *Athrotaxis cupressoides* is the only species that agrees in all respects—the arrangement and shape of the leaves and in the various features of the cuticles.

The present material agrees with that described by Halle (1913) from Río de los Fósiles, Santa Cruz Province, Argentina, of probable Lower Cretaceous age. The leaves are similar in arrangement, size and shape (the Ticó specimens are somewhat acute as in Halle's pl. 2, fig. 11, rather than as in some of his other figures). Un-

fortunately Halle's specimens have lost their cuticles, but they possess female cones similar to those of *A. cupressoides*. I was able to examine this material in the Stockholm Riksmuseum and I agree with Florin's interpretation, that it is closely similar to *A. cupressoides* (Florin, 1940).

The fossils from Lago San Martín are probably the same age as those from Ticó. The presence of the genus *Athrotaxis* in Upper Mesozoic floras of Patagonia, based on leaf cuticles, is another factor in favour of correlating both floras. The area between Lago San Martín and Ticó has not yet been thoroughly surveyed. There are some scattered references (Piatnitzky, 1938 : 64) about the finding of *Athrotaxis* near Lago Cardiel, but this should be verified by a more detailed survey of this extensive area.

Genus *TOMAXELLIA* nov.

DIAGNOSIS. Shoots of ultimate order bearing leaves spirally arranged, persistent, spreading, acicular, rhomboidal in section, acute at their apices, slightly decurrent at the base, amphistomatic, margins entire. Leaf cuticles thick. Cell walls straight, cell surface not papillose ; trichomes absent. Stomata widespread on abaxial cuticle, but avoiding margins, present on lower angle, not arranged in definite bands and forming ill-defined rows. Stomata on decurrent part of abaxial side irregularly distributed, not forming bands or rows. Stomata on adaxial cuticle, at base, forming ill-defined bands, then spread over whole surface, including median angle and lateral margins. Stomata present near apex, irregularly spaced, obliquely or longitudinally orientated, rarely transversely, sometimes side by side, never sharing subsidiary cells, haplocheilic and typically monocyclic or imperfectly dicyclic, with guard cells slightly sunken, surrounded by 4-5 subsidiary cells not well differentiated into polar and lateral. Subsidiary cells thickened near mouth of pit, with ridges parallel to margins of pit. Encircling cells sometimes with similar ridges. Anticlinal walls of subsidiary and encircling cells strongly cutinized. Hypodermal cells markedly elongated, cutinized.

TYPE SPECIES. *Tomaxellia degiustoi* sp. n.

DISCUSSION. *Tomaxellia* is a coniferous genus unrelated to the living and fossil Taxopsida. It can only be compared with some living genera belonging to the Podocarpaceae, Taxodiaceae, and in some degree to the Araucariaceae. It bears no relation or similarity to any other family of the Coniferales.

Similar genera belong to the Taxodiaceae, which have amphistomatic leaves, with four definite bands of stomata that are not arranged in definite rows but are indistinctly orientated. Some genera of this family have leaves similar in shape, size and insertion (*Cryptomeria* and *Athrotaxis*) but in these two genera the cuticular structure is rather different from that of *Tomaxellia*. On the other hand, some conifers having similarities with *Tomaxellia* in cuticular structure, have leaves of a different shape (*Taxodium*, *Sequoia sempervirens*). *Sequoia gigantea* (*Sequoia-dendron*) has similar leaves, but the stomata, which agree in that they are arranged in definite rows and are widely scattered as in *Tomaxellia*, usually form rather definite bands. In this respect *Tomaxellia* also differs from *Araucaria*, in which the stomata are always aggregated in compact rows, but certain species of *Araucaria* have leaves

of similar shape as well as similar stomatal apparatus. *Agathis*, on the other hand, has leaves of a different shape and a different cuticular structure.

All genera in the family Podocarpaceae differ from *Tomaxellia* in the shape of their leaves, with the exception of some species of *Dacrydium* which agree with *Tomaxellia* in the size, shape and disposition of leaves on the branches. They differ, however, from *Tomaxellia* in that the stomata form definite bands and are often arranged in rows. The stomata are longitudinally orientated and their details are rather different.

Bellarinea Florin (1952 : 179) is a Jurassic genus from Australia which resembles some living *Podocarpus* of the section *Stachycarpus*. *Tomaxellia* differs from *Bellarinea* in many respects. Its leaves are spirally disposed but not expanded in one plane. In *Bellarinea* the leaves are hypostomatic while in *Tomaxellia* they are amphistomatic. The stomatiferous bands are much more marked in the Australian genus than in ours.

Of the fossil Taxodiaceae, *Elatides*, as defined by Harris (1953) is similar to *Tomaxellia* in leaf shape. The differences lie in the bands of stomata and in their orientation, usually transverse in this genus. Also, the pits of the stomata are rectangular in shape, while those in *Tomaxellia* are always oval.

Sphenolepis, another member of the fossil Taxodiaceae, differs from *Tomaxellia* in the shape of leaves (scale-like), in their hypostomatic condition, and in the stomata which do form bands, are transversely elongated and typically monocyclic.

The fossil genus *Elatocladus* is a comprehensive and unnatural one. It includes many species which differ from *Tomaxellia* in being mainly hypostomatic. The few amphistomatic species of *Elatocladus* are very different from *Tomaxellia* in their stomatal apparatus and general epidermal structure.

The only known Taxodiaceae from the Mesozoic floras of Patagonia (with the exception of *Athrotaxis ungeri*) is *Pararaucaria patagonica* Wieland from the Matilda Formation of Santa Cruz Province, the age of which is Middle to Upper Jurassic. It is based on a female cone related to *Cryptomeria* and *Taiwania* on the one hand, and the most typical Taxodiaceae on the other (Calder, 1953). It could well be that *Tomaxellia* is related to *Pararaucaria*; there is no great difference either in age or locality.

As far as I am aware, *Tomaxellia* differs from all other Jurassic or Lower Cretaceous conifer genera which have been described with their cuticles. On the evidence available no definite relationship between *Tomaxellia* and the Taxodiaceae, Podocarpaceae or Araucariaceae can be maintained.

The genus is dedicated to Professor Thomas Maxwell Harris of Reading University, England.

Tomaxellia degiustoi sp. n.

(Pl. 7, figs. 39, 40; Pl. 8, figs. 58–60; Pl. 11, Pl. 12, fig. 79; Text-figs. 72–74)

DIAGNOSIS (Plant known only from isolated and fragmentary branches). Ultimate (?) branches, 1–2 mm. in diameter, bearing spirally attached leaves of probably 2/5 phyllotaxis. Leaf cushions small, oval or rhomboidal, 2 mm. long \times 1 mm.

broad. Leaves long and narrow, slightly decurrent, almost acicular, typically 1 cm. long \times 1-1.5 mm. wide and 1.5 mm. thick, ending with acute apex, pointing forward and projecting towards the stem. Free part of leaf rhomboidal in transverse section but upper and lower angles somewhat rounded, and in middle region of leaf, lower angle bearing wide short papillae. Lateral angles sharp, entire.

Cuticle thick, up to 8 μ . Stomata present on both cuticles. On decurrent part, stomata irregularly distributed, not forming rows or bands. Towards the middle part of leaf, on abaxial cuticle, stomata forming irregular bands. On adaxial cuticle, irregular bands sometimes marked from the base. On lower cuticle, stomata markedly avoiding margins (lateral angles) leaving a non-stomatiferous band sometimes more than 10 cells wide. Median region (lower angle) with 2-3 narrow and markedly elongated rows of cells, sometimes with 1 or 2 bands of strongly cutinized cells which may bear short and round single papillae. When two of these bands are present, very elongated stomata can be found between (i.e. actually on the lower angle). On upper cuticle stomata indistinctly present near margins or median region. On apical part stomata becoming fewer but reaching apex. Bands ill-defined, sometimes marked up to near apex. Stomata typically obliquely or longitudinally orientated, sometimes transversely. Stomata in bands sometimes forming ill-defined rows separated by typically 2-4 rows of elongated rectangular cells. Stomata when in a row, usually separated, sometimes having their lateral encircling cells in contact (in oblique or transverse stomata) but never sharing subsidiary cells.

Epidermal cells located on same rows as stomata, usually elongated in longitudinal or transverse direction, rarely isodiametric. Epidermal cells between stomatiferous rows, bands and on margins, elongated, rectangular, typically 60-100 μ long \times 15 μ wide. Near leaf apex, epidermal cells unpitted, flat, but with low median ridge, sometimes with extensions towards corners of cells, and often with faint longitudinal striae. Lateral and end walls of cells straight, strongly marked, unpitted, without borders.

Stomata similar on both cuticles, typically monocyclic or imperfectly dicyclic, rarely perfectly dicyclic. Stomatal apparatus usually oval, rarely circular (never rectangular). Guard cells slightly sunken in oval pit, very feebly cutinized, surrounded by typically 4-5 subsidiary cells. Subsidiary cells small and inconspicuous in dicyclic stomata, larger in monocyclic, with their anticlinal walls strongly cutinized. Polar and lateral subsidiary cells not well differentiated. Mouth of pit oval. Subsidiary cells and sometimes encircling cells with one or more ridges parallel to mouth of pit.

Hypodermal cells cutinised, markedly elongated.

HOLOTYPE.—LIL PB n. 2542(b). The same specimen as *Ruflorinia sierra*.

MATERIAL.—In addition to the holotype, Brit. Mus. (Nat. Hist.) no. V.44661. Slides: LIL 229-232.

DESCRIPTION.—This species comes from the *Ticoa harrisii* bed. It is not as common as the other two conifers described from the same bed (*Brachyphyllum brettii*, *B. mucronatum*). The two specimens so far available are fragmentary. In the matrix, however, detached leaves are often found. The leaves are long, almost acicular, somewhat falcate. The cuticle of the leaves is well preserved. The lower

cuticle is always wider than the upper, making the leaf kite-shaped in section. Both cuticles have a median longitudinal zone where they fold, having thus 4 definite areas. On the lower cuticle, this median fold is always marked by a band of strongly cutinized cells which do not occur on the upper cuticle. The shape of the leaf may have been somewhat similar to the living *Cryptomeria japonica*, *Araucaria columnaris*, *Dacrydium balansae* and *D. araucarioides*.

In no case was there any indication of a sharply marked stomatiferous band. On the upper cuticle the stomata are dispersed and very seldom form rows. On the lower cuticle the two non-stomatiferous bands are obvious near the margins. On the rest of the lamina the stomata have the same arrangement as on the upper cuticle.

The interpretation of the stomata is not easy, because there are numerous ridges on the subsidiary and encircling cells which can be confused with cell walls. However, using the phase contrast microscope, it was possible to distinguish between the true cell walls and the ridges. The anticlinal walls of subsidiary cells are strongly cutinized and often have the same thickness as the ridges present on the cell surface.

The leaves of *Tomaxellia degiustoi* are somewhat similar in shape and arrangement to those of some living Araucariaceae, Taxodiaceae and Podocarpaceae, for example *Araucaria columnaris* and *A. excelsa*. *Tomaxellia* differs from them, however, in the distribution of stomata. In *Araucaria* the stomata are not arranged in bands, they are crowded in definite rows.

The arrangement of stomata in 4 definite bands is characteristic of most Taxodiaceae; this feature is not shared by *Tomaxellia degiustoi* in which the stomatal rows are ill-defined. However, our genus is closer to the Taxodiaceae than to any other family, because in neither do the stomata form definite rows but are indefinitely orientated. In both Araucariaceae and Taxodiaceae the stomata tend to be crowded (dense), while in *Tomaxellia* they are markedly spaced.

In the Podocarpaceae, *Dacrydium balansae* and *D. araucarioides* from New Caledonia, are comparable to *Tomaxellia* in shape and size of leaves (the long leaved forms). The individual leaves are, however, somewhat more falcate. In both species, the leaves are amphistomatic, but in *D. araucarioides* the stomatiferous bands on the lower cuticle are ill- or not at all defined, and are only present on the decurrent part of the epidermis and a short way up the lamina. In addition the stomata are orientated longitudinally. In *Dacrydium gibbsiae* from Borneo, the stomata on the upper epidermis do not form bands, but longitudinal rows, reaching to the apical part of the leaf. On the lower epidermis stomata are present only on the basal part where they form short rows. All stomata are longitudinally orientated. The size and shape of leaves are comparable with *Tomaxellia* but they are more crowded on the branch.

The stomatal apparatus of *Tomaxellia* is comparable to some species of *Araucaria*, in being partially dicyclic; but the guard cells in *Araucaria* are usually more sunken. Strong ridges on subsidiary cells and encircling cells present in *Tomaxellia* are not common in *Araucaria*. In the Taxodiaceae, a comparable stomatal apparatus is found in *Sequoia sempervirens* and *S. gigantea* (*Sequoiadendron*) but with no marked

ridges on subsidiary cells as in *Tomaxellia*. The stomal apparatus of most *Dacrydium* species is rather different. There is a marked tendency for polar subsidiary cells to be differentiated from lateral ones and often the polar cells of two neighbouring stomata are in contact or are shared one per two adjacent stomata. In *Tomaxellia* the polar and lateral subsidiary cells of stomata are not differentiated. Furthermore, the ridges parallel to the pit are strongly developed. Such ridges do not appear to be present in the living species of *Dacrydium*.

As far as comparison with fossil genera goes, some features are shared with *Elatides williamsoni*. The size, shape and insertion of leaves are similar. The cuticle of *E. williamsoni* is much thinner and has definite bands of stomata, while no such bands exist in *Tomaxellia*. In both species the stomata are irregularly orientated. *Elatides bommeri* Harris (1953) has smaller leaves which have stomata only on one side (adaxial), forming two bands. The stomata of this species are usually transversely orientated.

Comparing *Tomaxellia* with fossil species of *Elatocladus* with their cuticles preserved, one almost constant feature is the hypostomatic condition of the latter species. *E. areolatus* Florin (1958) from the Jurassic of Yorkshire is amphistomatic and the very few stomata on the upper side appear to be functionless. There are also other differences such as the papillae present on the epidermal cells, and sometimes wavy walls of cells. The stomatal apparatus is also different.

Harris (1935) described several species of *Elatocladus* from East Greenland, three of them being amphistomatic. The stomatal apparatus of these species is quite different from that of *Tomaxellia*.

The specimens described as *Elatocladus heterophylla* Halle by Menéndez (1956) from the Jurassic of Neuquén, Argentina, have smaller leaves than those of *Tomaxellia* and they are closer to the shoot. There is no information about the stomata. The typical forms of this species were described by Halle (1913) from Graham Land. They are preserved as impressions. I have re-examined all Halle's specimens and the one most similar to our species is figured in his pl. 8, fig. 22a. There is no difference in shape and size of leaves of the two species, but in Halle's specimen the leaves are expanded in one plane as in many species of the living genus *Podocarpus* whilst in *Tomaxellia*, the leaves are directed towards all sides. It is interesting to note that Florin (1940) considers that all *Elatocladus* species described by Halle have Podocarpaceous affinities. *Elatocladus* has definitely dimorphic leaves. Although our material is very fragmentary, in none of the fragments, nor in the numerous detached isolated leaves is there any indication whatsoever that *Tomaxellia* has dimorphic leaves.

The species is dedicated to Dr. José M. de Giusto, geologist of the National Oil Company (YPF).

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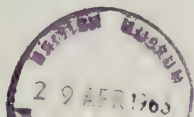
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PLATE I

Ticoa magnipinnulata sp. n.

FIG. 1. Holotype. (LIL 2540.) $\times 1$.

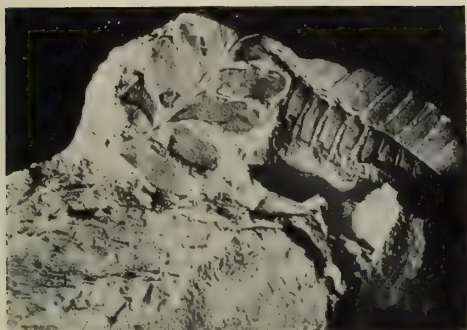
FIG. 3. Upper cuticle of a pinnule showing only trichome bases and no stomata. (Slide LIL 165.) $\times 17.5$.

FIG. 4. Lower cuticle of rachis and bases of three pinnules. Non-stomatiferous bands with trichome bases correspond to veins. Stomata seen as conspicuous black dots. (Slide LIL 166.) $\times 15$.

Ticoa harrisii gen. et sp. n.

FIG. 2. Two pinnae and rachis showing the two compressed flanges. (Slide LIL 164.) $\times 3$.

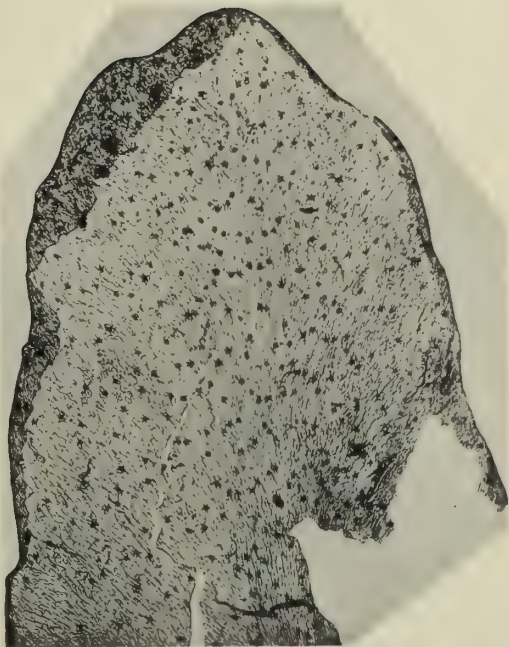
FIG. 5. Lower cuticle of a pinna showing the non-stomatiferous bands (veins) and the general distribution of stomata and trichome bases. (Slide LIL 161.) $\times 15$.



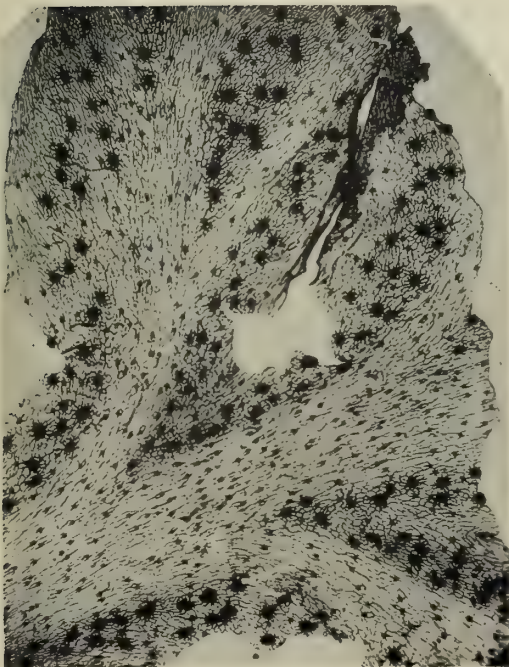
1



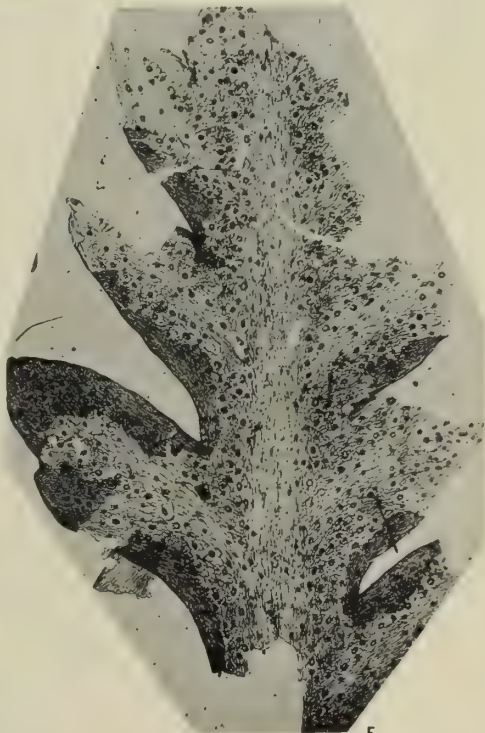
2



3



4



5

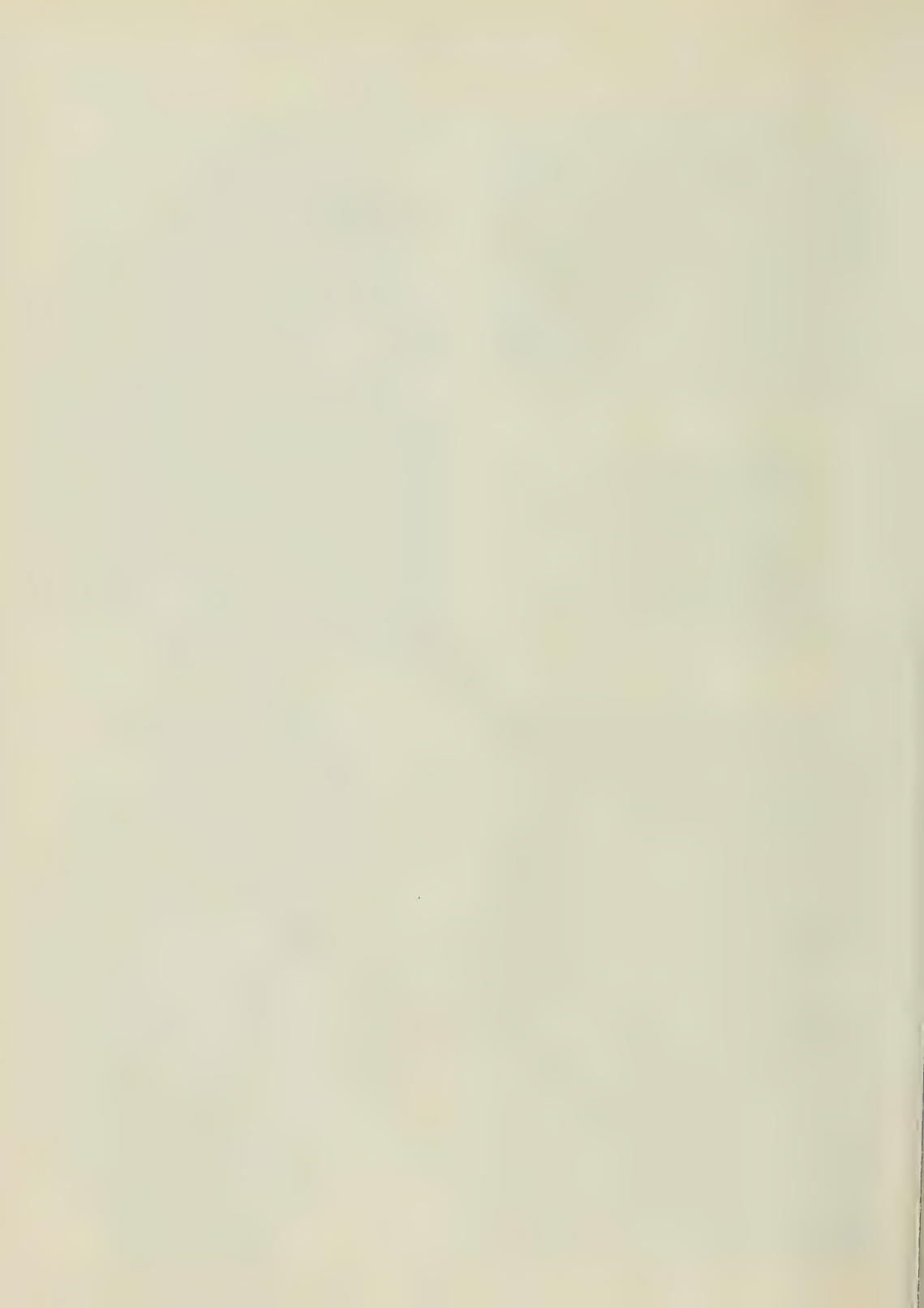


PLATE 2

Ticoa magnipinnulata sp. n.

FIG. 6. Lower cuticle showing stomatiferous bands (stomata seen as conspicuous black dots). (Slide LIL 167.) $\times 15$.

Ticoa harrisii gen. et. sp. n.

FIG. 7. Upper and lower cuticles of two pinnules. Above (upper cuticle) only bases of trichomes are seen. (Slide LIL 160.) $\times 40$.

Ruflorinia sierra gen. et sp. n.

FIG. 8. Lower cuticle showing patches of stomata. (Slide LIL 171.) $\times 40$.

FIG. 9. Lower cuticle showing rachis and decurrent pinnules. Bands of stomata can be seen. (Slide LIL 170.) $\times 15$.



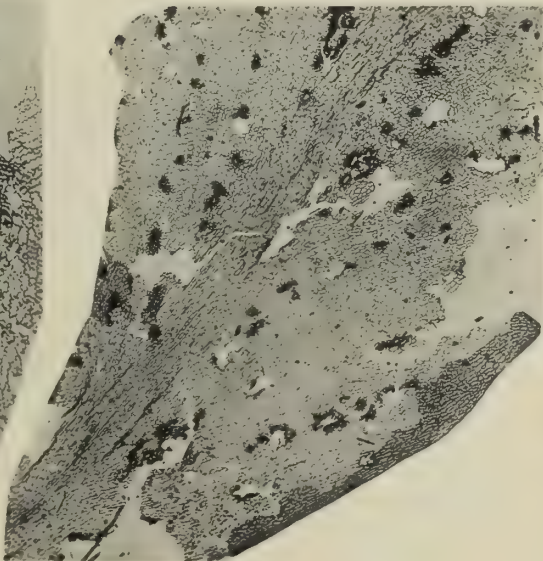
6



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9

PLATE 3

Mesosingeria coriacea gen. et sp. n.

FIG. 10. Upper and lower cuticles ; the lower (left) with stomata. (Slide LIL 173.) $\times 40$.

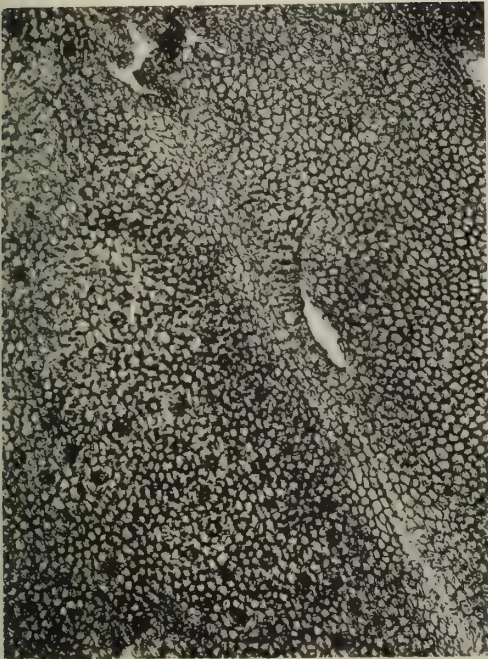
Mesosingeria herbstii sp. n.

FIG. 11. Upper and lower cuticles ; lower cuticle (left) having more stomata than upper. (Slide LIL 175.) $\times 40$.

Mesodescolea plicata gen. et sp. n.

FIG. 12. Lower cuticle showing stomata. (Slide LIL 177.) $\times 200$.

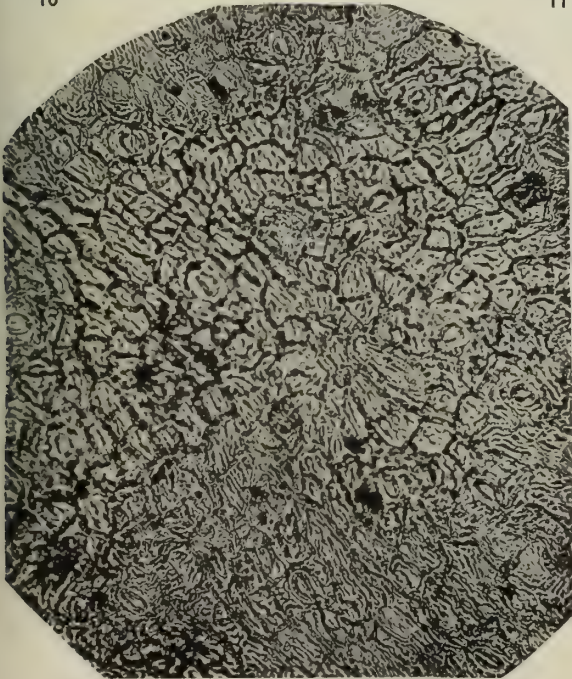
FIGS. 13, 14. Upper cuticle with no stomata. (Slide LIL 178.) $\times 200$.



10



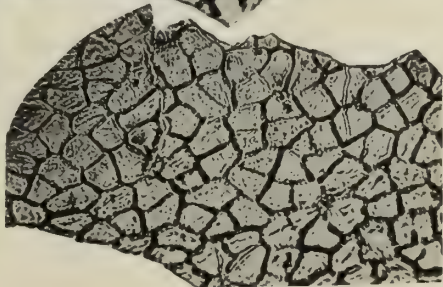
11



12



13



14

PLATE 4

Ticoa harrisii gen. et sp. n.

FIGS. 15, 16. Lower cuticle. Stoma focused at two different levels to show mouth of pit (Fig. 15) and guard cells (Fig. 16). (Slide LIL 160.)

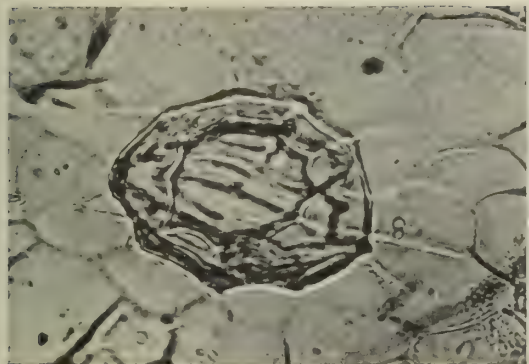
FIG. 20. Lower cuticle showing base of a trichome. (Slide LIL 160.)

Ticoa magnipinnulata sp. n.

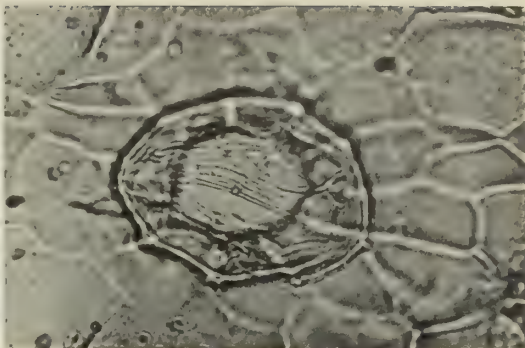
FIGS. 17, 18. Lower cuticle. A stoma focused at two different levels to show mouth of pit (Fig. 17) and guard cells (Fig. 18). (Slide LIL 167.)

FIG. 19. Lower cuticle. Stoma focused at a level between mouth of pit and guard cells, showing several cycles of subsidiary cells. (Slide LIL 167.)

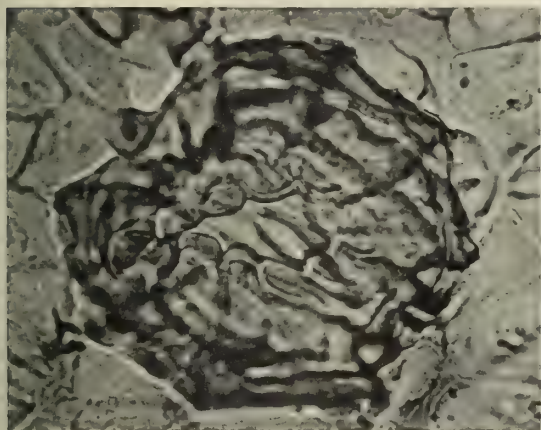
All $\times 500$.



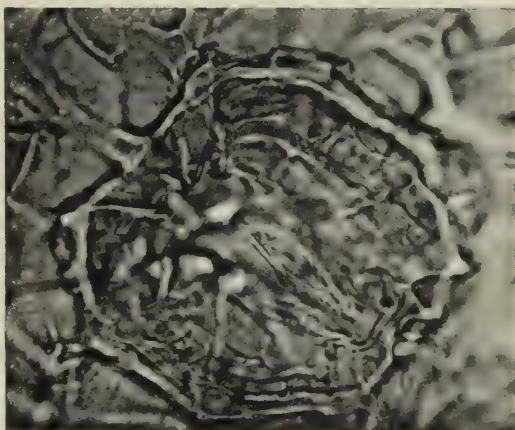
15



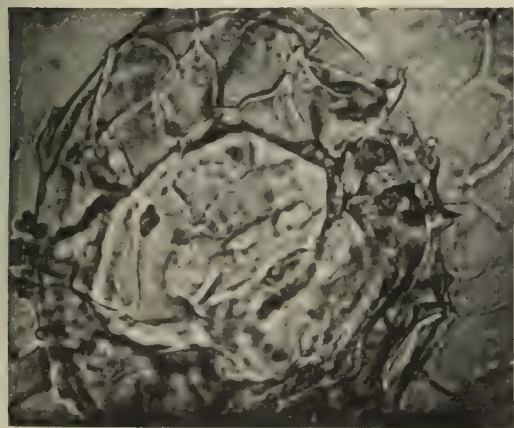
16



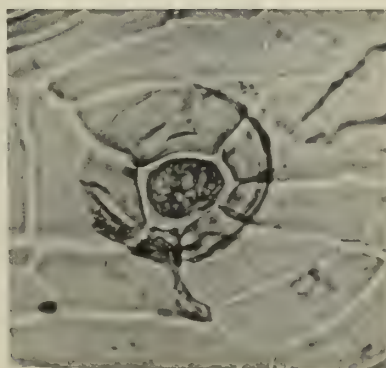
17



18



19



20

PLATE 5

Ruflorinia sierra gen. et sp. n.

FIG. 21. Lower cuticle. Stoma showing papilla-like projections over mouth of pit. (Slide LIL 170.) $\times 500$.

Mesosingeria coriacea gen. et sp. n.

FIGS. 22, 23. Lower cuticle. Stoma focused at two different levels showing the mouth of pit and the guard cells slightly out of focus (Fig. 22) and the rim of cutin at the uppermost level (Fig. 23). (Slide LIL 173.) $\times 600$.

Mesodescolea plicata gen. et sp. n.

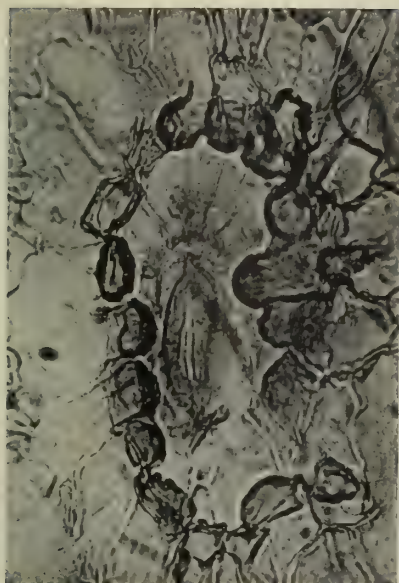
FIG. 24. Lower cuticle. Stoma with oval rim of cutin. (Slide LIL 177.) $\times 600$.

FIG. 25. Lower cuticle. Trichome base showing strong radiating striae. (Slide LIL 177.) $\times 600$.

Mesosingeria herbstii sp. n.

FIG. 26. Lower cuticle. Stoma showing mouth of pit and, slightly out of focus, the rim of cutin projecting outwards. (Slide LIL 175.) $\times 500$.

FIG. 27. Lower cuticle. Two hairs. (Slide LIL 175.) $\times 500$.



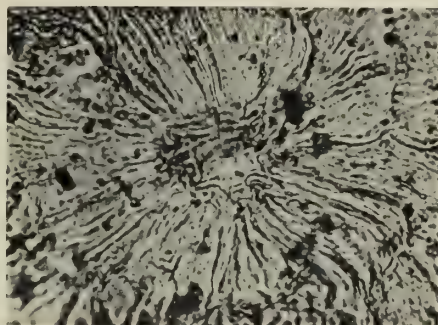
21



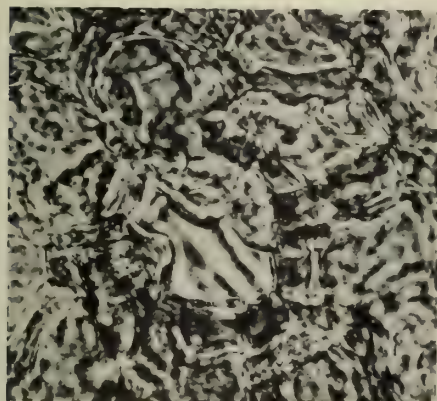
24



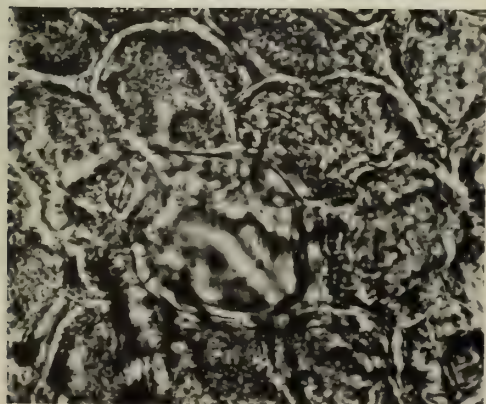
26



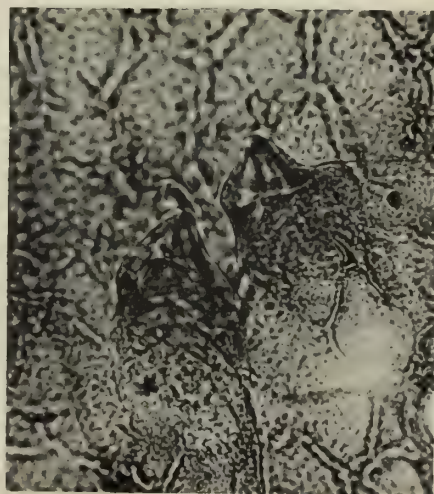
25



22



23



27

PLATE 6

Ktalenia circularis gen. et sp. n.

FIG. 28. General aspect of the holotype. (Slide LIL 181.) $\times 15$.

FIG. 29. Seed showing nucellus and integument membranes. At bottom chalaza and at top micropilar canal. (Slide LIL 182.) $\times 15$.

FIG. 30. Seed showing nucellus membrane. At the bottom, chalaza (black). At the top, micropilar canal (somewhat obliterated) and integument membrane. (Slide V.44687.) $\times 15$.

FIG. 31. Magnification of Fig. 29 showing the top of the nucellus with cutinized micropilar canal and integument membrane. $\times 60$.

FIG. 32. Circular bodied inside cuticle of nucellus, probably oily endosperm. (Slide LIL 183.) $\times 60$.

FIG. 33. Cuticle of the fruit wall showing an opening. (Slide LIL 182.) $\times 40$.

Tomaxellia degiustoi gen. et sp. n.

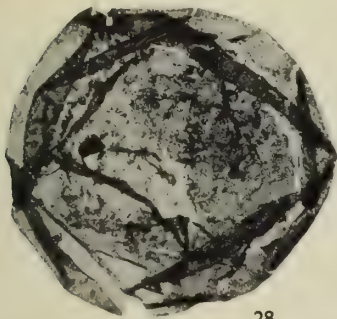
FIG. 34. Median part of leaf showing the longitudinal division in four sectors. The dark longitudinal band on the lower left corresponds to a strong cutinized ridge separating the two sectors of the lower cuticle. (Slide LIL 229.) $\times 40$.

Athrotaxis ungeri (Halle)

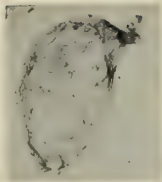
FIG. 35. General aspect of a leaf showing dentate margins, some papillae on the base and a portion of the upper cuticle at the top. (Slide LIL 228.) $\times 40$.

Mesosingeria herbstii gen. et sp. n.

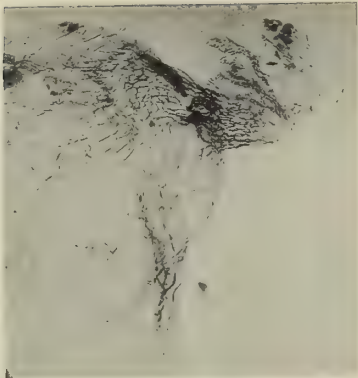
FIG. 36. Lower cuticle showing stoma. The opening of the slender cutin rim projecting upwards is seen. On a lower level, the mouth of the pit is also seen. (Slide LIL 175.) $\times 600$.



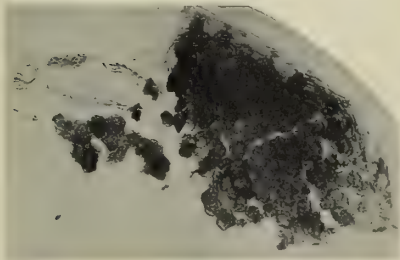
28



29



31



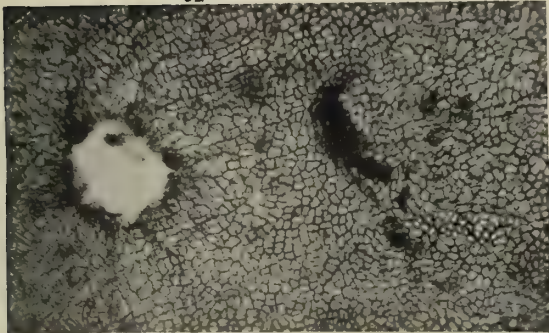
32



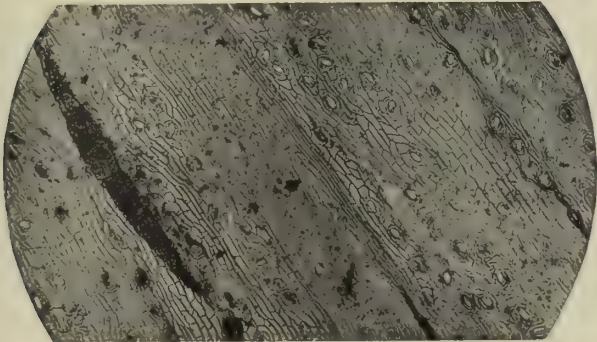
30



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33



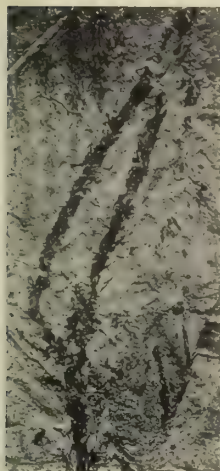
34



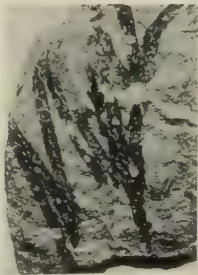
36

PLATE 7

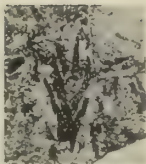
- FIG. 37. *Brachyphyllum brettii* sp. n. A branched twig. V.44686. $\times 1$.
- FIG. 38. *Brachyphyllum brettii* sp. n. Holotype. (LIL 2565.) $\times 1$.
- FIG. 39. *Tomaxellia degiustoi* gen. et sp. n. Fragmentary twig. V.44661. $\times 1$.
- FIG. 40. *Tomaxellia degiustoi* gen. et sp. n. Holotype. (LIL 2542.) $\times 1$.
- FIG. 41. *Brachyphyllum mirandai* sp. n. Holotype. (LIL 2560.) $\times 1$.
- FIG. 42. *Athrotaxis ungeri* (Halle). General aspect of small fragmentary twigs. (LIL 2563.) $\times 1$.
- FIG. 43. *Brachyphyllum mucronatum* sp. n. Holotype. (LIL 2569.) $\times 1$.
- FIG. 44. *Brachyphyllum irregulare* sp. n. General aspect of fragmentary twigs. (LIL 2579.) $\times 1$.
- FIG. 45. Male cone. Longitudinal compression. (LIL 2562.) $\times 3$.
- FIG. 46. Pollen grain. (Slide LIL 221.) $\times 1000$.



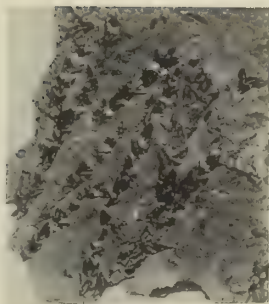
37



38



39



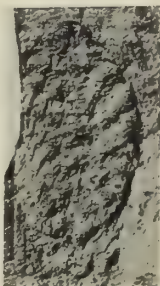
41



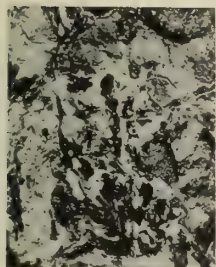
40



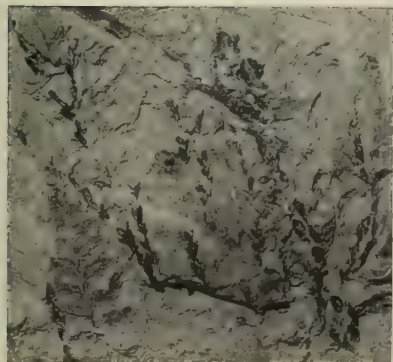
43



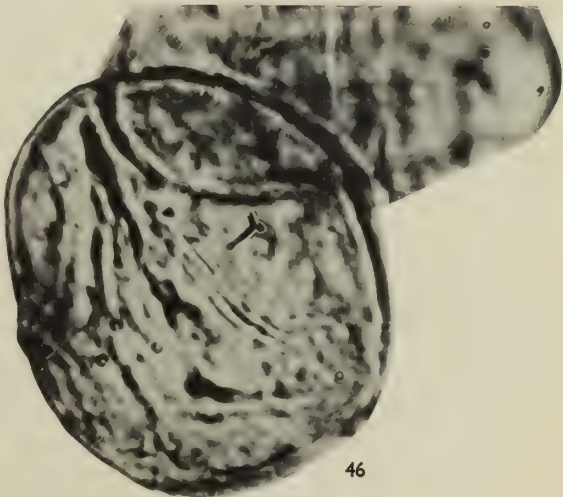
45



42



44



46

PLATE 8

FIGS. 47-49. *Brachyphyllum brettii* sp. n. Small leaves. (Slide LIL 188.) $\times 8$.

FIG. 50. *Brachyphyllum brettii* sp. n. A large leaf. (Slide LIL 186.) $\times 8$.

FIGS. 51, 52. *Brachyphyllum mucronatum* sp. n. Leaves of normal size. (Slide LIL 200.) $\times 8$.

FIGS. 53, 54. *Brachyphyllum mirandai* sp. n. Small and normal leaves. (Slide LIL 215.) $\times 8$.

FIG. 55. *Brachyphyllum mirandai* sp. n. A large leaf. (Slide LIL 216.) $\times 8$.

FIGS. 56, 57. *Brachyphyllum irregulare* sp. n. Leaves of normal size. (Slide LIL 225.) $\times 8$.

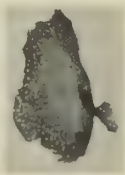
FIG. 58. *Tomaxellia degiustoi* gen. et sp. n. Complete leaf showing the longitudinal division into four parts. (Slide LIL 229.) $\times 9$.

FIG. 59. *Tomaxellia degiustoi* gen. et sp. n. Complete leaf showing irregular distribution of stomata in the decurrent part of lower cuticle. (Slide LIL 232.) $\times 8$.

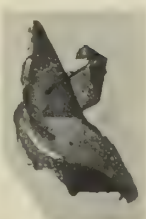
FIG. 60. *Tomaxellia degiustoi* gen. et sp. n. Leaf showing stomatiferous bands in the middle and top of lamina. (Slide LIL 229.) $\times 9$.



47



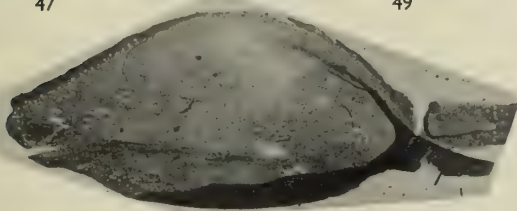
48



49



55



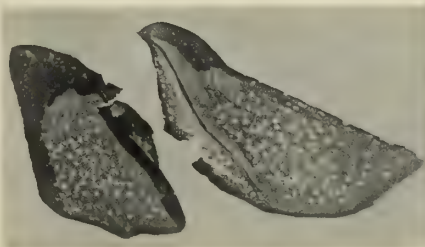
50



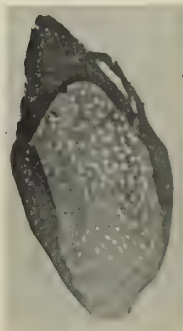
51



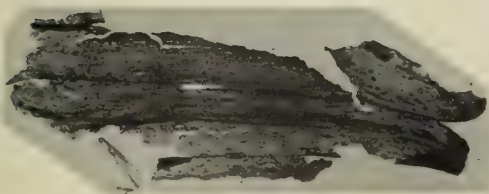
52



53



54



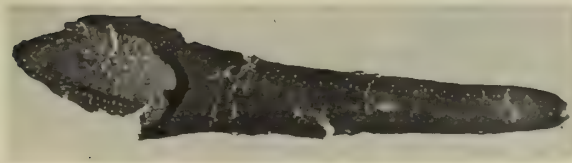
58



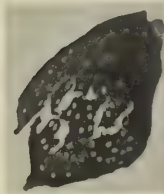
56



60



59



57

PLATE 9

Brachyphyllum mirandai sp. n.

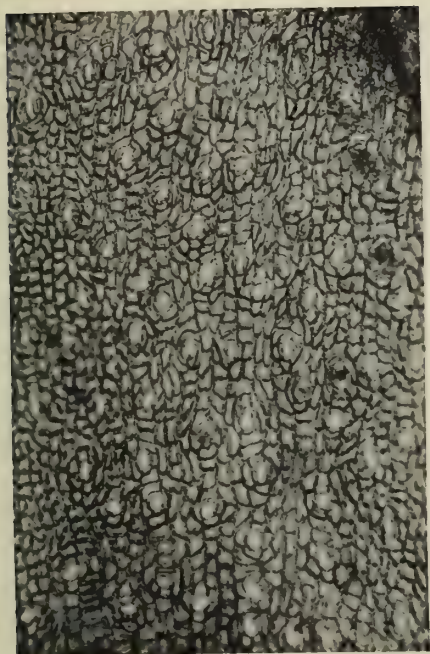
FIG. 61. General aspect of lower cuticle showing distribution of stomata. (Slide LIL 215.)
×50.

FIG. 62. Leaf margin showing elongated marginal cells. (Slide LIL 215.) ×500.

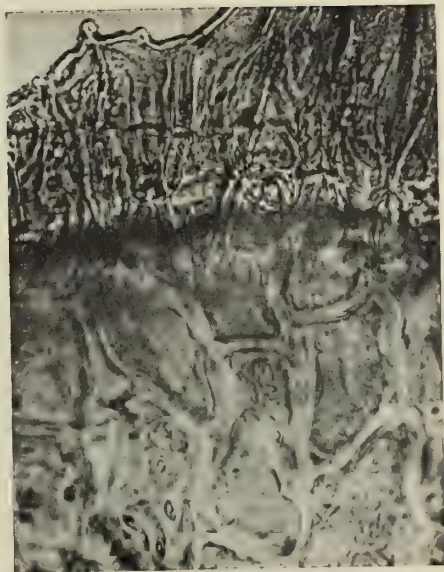
Brachyphyllum brettii sp. n.

FIG. 63. Apical part of leaf showing the marginal elongated cells along the whole length of upper cuticle. (Slide LIL 195.) ×50.

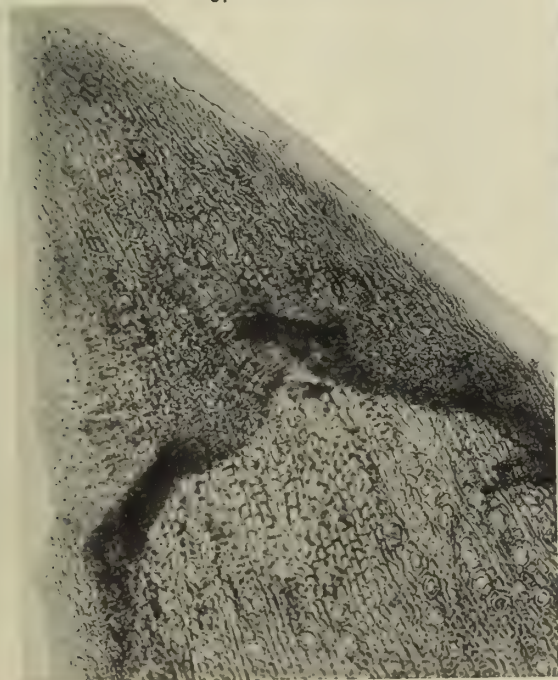
FIG. 64. General aspect of lower cuticle showing distribution of stomata tending to form longitudinal rows. (Slide LIL 188.) ×50.



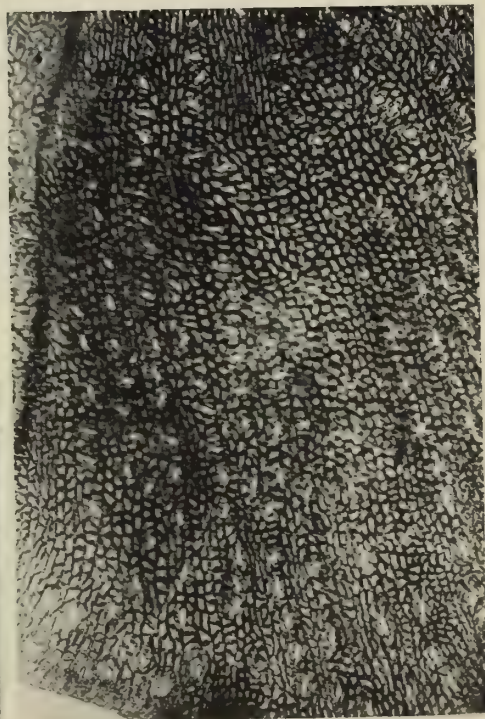
61



62



63



64

PLATE 10

Brachyphyllum irregulare sp. n.

FIG. 65. General aspect of lower cuticle showing distribution of stomata. (Slide LIL 225.)
× 50.

Brachyphyllum mucronatum sp. n.

FIG. 66. General aspect of lower cuticle showing distribution of stomata. (Slide LIL 201.)
× 50.

Athrotaxis ungeri (Halle)

FIG. 67. Basal part of lower cuticle showing papillae and elongated marginal cells. (Slide LIL 228.) × 100.

FIG. 68. General aspect of lower cuticle. (Slide LIL 228.) × 40.

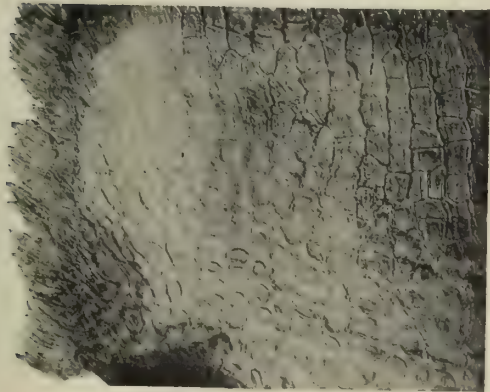
FIG. 69. Upper cuticle showing some stomata. (Slide LIL 228.) × 50.



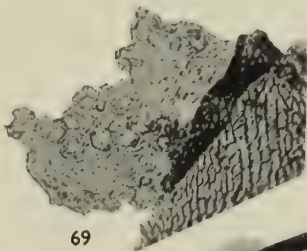
65



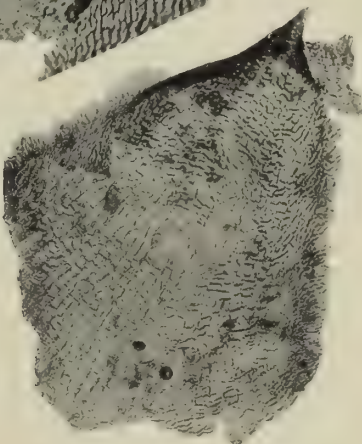
66



67



69



68

PLATE 11

Tomaxellia degiustoi gen. et sp. n.

FIG. 70. Apical part of leaf (upper and lower cuticles). (Slide LIL 231.)

FIG. 71. Median part of leaf showing the longitudinal division into four parts, the two upper parts correspond to the upper cuticle. (Slide LIL 229.)

FIG. 72. Margin of leaf separating lower cuticle (left) from upper one (right). (Slide LIL 229.)

FIG. 73. Decurrent part of leaf (lower cuticle) showing irregular distribution of stomata. (Slide LIL 232.)

All $\times 50$.

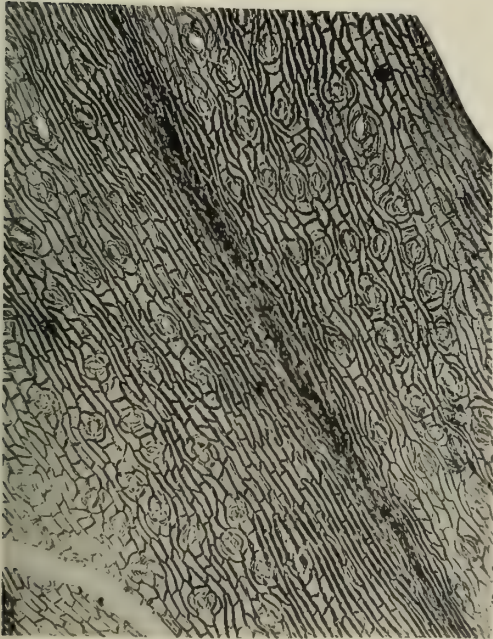
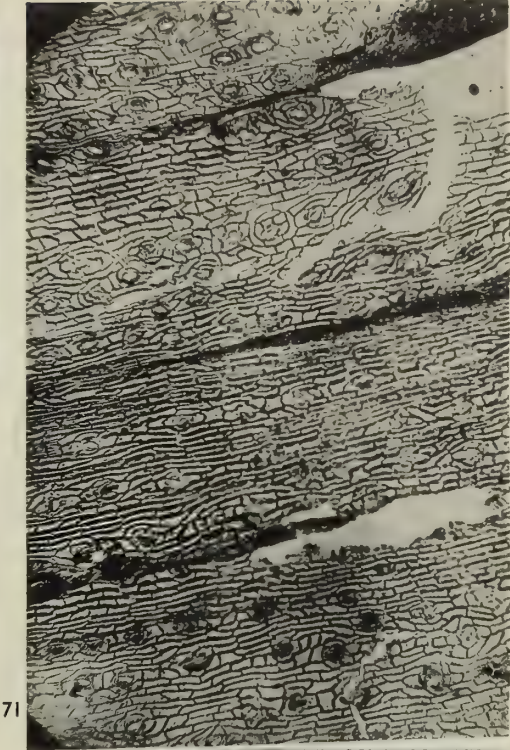
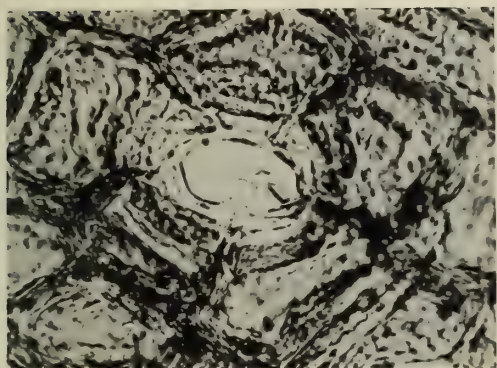


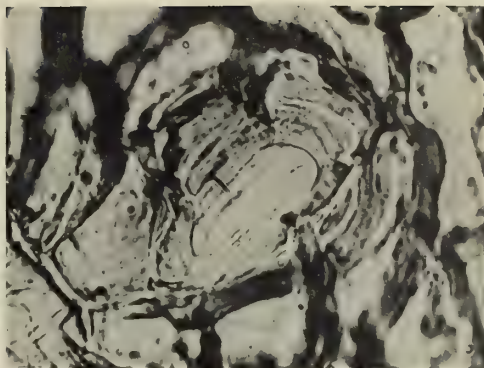
PLATE 12

STOMATA

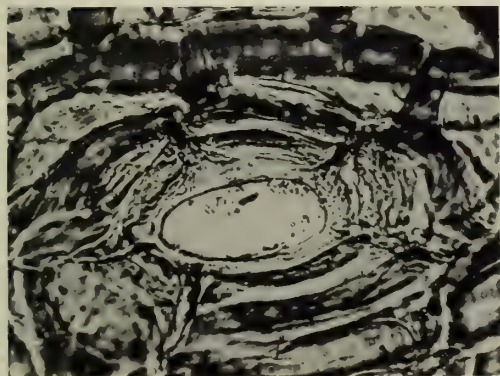
- FIG. 74. *Brachyphyllum brettii* sp. n. (Slide LIL 194.) $\times 500$.
FIG. 75. *Brachyphyllum mucronatum* sp. n. (Slide LIL 201.) $\times 500$.
FIG. 76. *Brachyphyllum mirandai* sp. n. (Slide LIL 215.) $\times 350$.
FIG. 77. *Brachyphyllum irregulare* sp. n. (Slide LIL 225.) $\times 350$.
FIG. 78. *Athrotaxis ungeri* (Halle). (Slide LIL 228.) $\times 500$.
FIG. 79. *Tomaxellia degiustoi* gen. et sp. n. (Slide LIL 229.) $\times 500$.



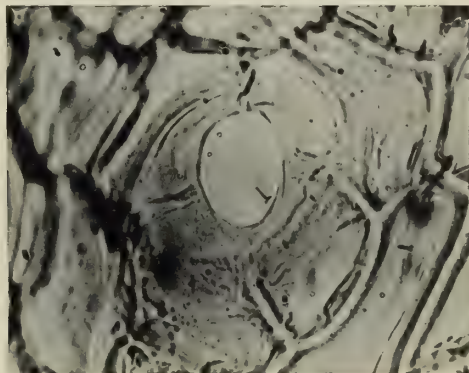
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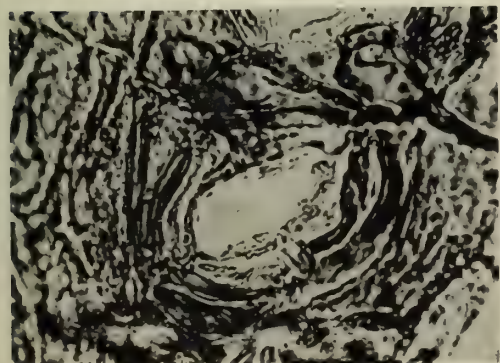
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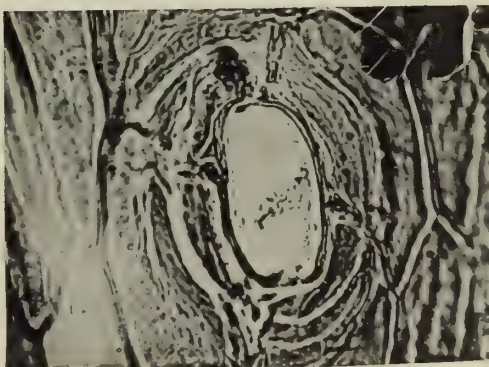
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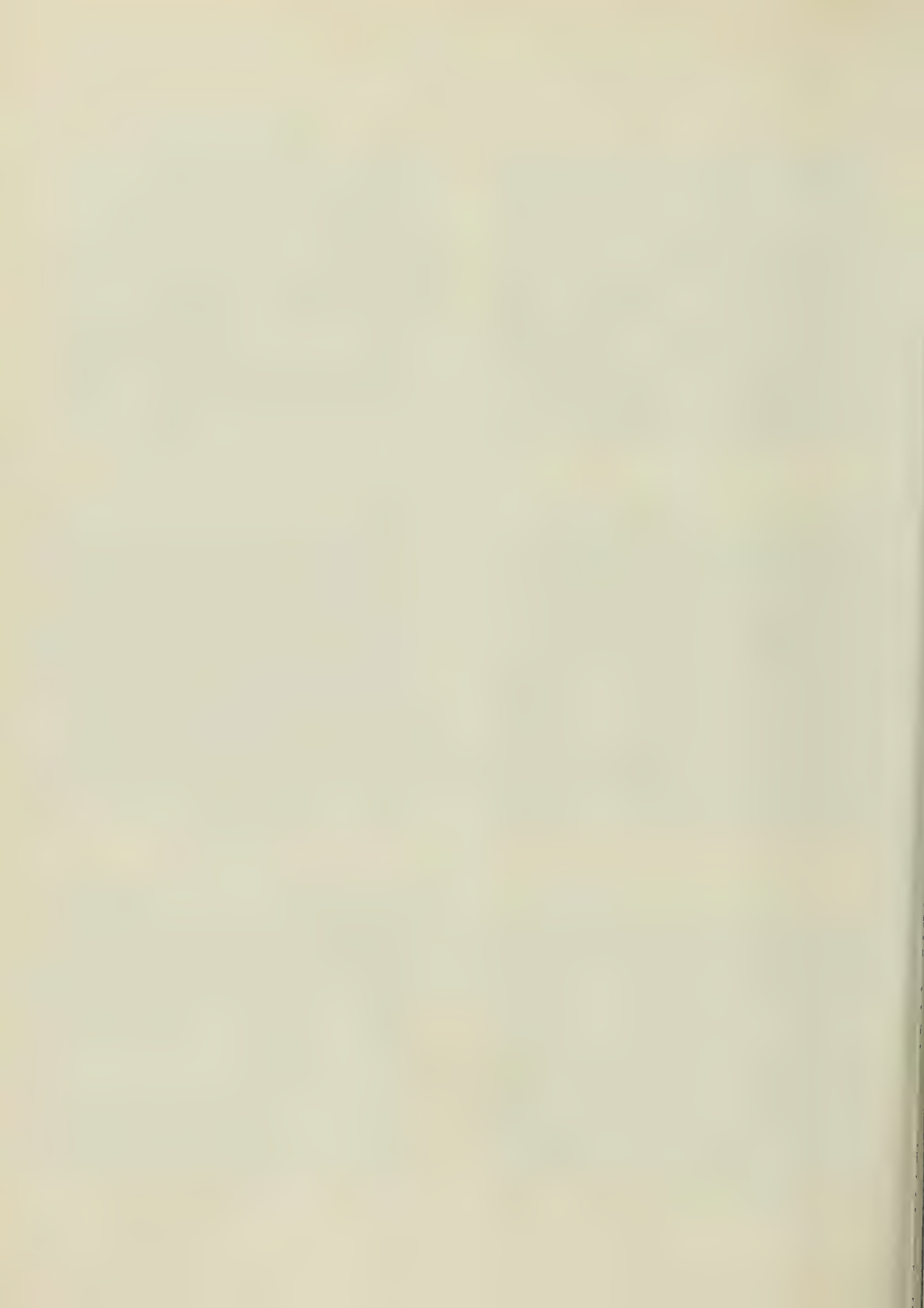
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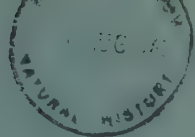


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THE SILURIAN ROCKS OF THE LUDLOW DISTRICT, SHROPSHIRE

C. H. HOLLAND, J. D. LAWSON

AND

V. G. WALMSLEY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 8 No. 3
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THE SILURIAN ROCKS OF THE LUDLOW
DISTRICT, SHROPSHIRE

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SYNOPSIS

The Silurian rocks of the Ludlow district have been re-mapped. The strata are folded into an asymmetrical anticline plunging east-north-eastwards. Of the two formations of the Wenlockian Series, the Wenlock Shales are of the typical shelf development but the Wenlock Limestone is more argillaceous and less fossiliferous than on Wenlock Edge. The Ludlovian Series comprises nine stratigraphical divisions recognized by faunal and, to a lesser extent, lithological criteria. A standard section is described for each boundary. Significant changes in lithology and fauna take place at some levels towards the west of the area, as the basin facies is approached.

The base of the Ludlovian Series is described at a standard section and four stages (Eltonian, Bringewoodian, Leintwardinian and Whitcliffian) are introduced. The boundaries between them are defined at standard sections. The base of the Downtonian Stage, and hence that of the Lower Old Red Sandstone Series, is also formally fixed at the base of the Ludlow Bone Bed at "Ludford Lane".

A correlation chart links the local Ludlovian successions in the Welsh Borderland and south-central Wales with this new classification for the type area.

I. INTRODUCTION

THE Ludlow district is historically important as the type area selected by Murchison for the Ludlow Series of his Silurian System. In recent years, most of the Ludlovian

strata of the Welsh Borderland have been re-mapped, and it was as a result of difficulties experienced when correlation with the type area was attempted, that the necessity for a revision of this area became clear.

A brief summary of the new classification has already been published (Holland, Lawson & Walmsley, 1959). Full details are now presented and four Ludlovian stages are introduced. Standard sections on which they are based, selected from the type area, are described in detail. The correlation chart of Welsh Borderland Ludlovian (shelf and basin facies) summarizes the authors' views.

The continuity of the north-east to south-west regional strike of the south-easterly dipping Silurian rocks of the main outcrop is broken in the Ludlow district by an asymmetrical anticline plunging east-north-eastwards. It is this denuded Ludlow Anticline which provides the type area.

In the core of the anticline the Wenlock Shale outcrop forms ground between 400 ft. and 500 ft. O.D., partly covered by river alluvium. The succeeding Wenlock Limestone gives rise to a V-shaped wooded scarp (see Plate 1) about 800 to 900 ft. O.D. overlooking the Wenlock Shale plain. Between the Wenlock Limestone scarp and the higher scarp feature formed normally by Bringewood Beds, the softer Lower and Middle Elton Beds form either a ledge or a valley. The wooded ridges of Bringewood Beds rising to 1,192 ft. on Bringewood Chase, 1,235 ft. on High Vinnalls, and over 1,000 ft. on Mary Knoll, fall away to the north, east and south in gentle dip slopes of higher Ludlovian strata towards the mainly flat-lying Downtonian outcrops which bound the area.

The area has been mapped on the following Six-inches to One Mile Ordnance Survey Sheets: Shropshire 77 S.E., 78 N.W., 78 N.E., 78 S.E., 78 S.W., 82 N.E. It is covered by the Ordnance Survey 1:25,000 Sheets SO 47 and SO 57 and the One-inch Sheet 129. The district is included on the Geological Survey Old Series One-inch Sheet 55 N.W.

In descriptions of lithology, the Rock Color Chart (1951) of the Geological Society of America, the Wentworth 1922 scale of grade and class terms for clastic sediments, and the bedding terms defined by Holland (1959: 451) have been used. Authors of Ludlovian fossil species are given in the List of Fossils (see p. 152).

Probably the earliest reference to the geology of the Ludlow district was by Wright (1832) who gave a general description of the "Secondary Formations" in this neighbourhood. Murchison (1833: 475) established the descending sequence of, I. Upper Ludlow rock ("named because the Castle of Ludlow stands upon it"), II. Wenlock Limestone (in which he apparently included the limestones of both Wenlock Edge and Aymestrey) and III. Lower Ludlow Rock. He suggested "the term Ludlow Formation (the upper and lower Ludlow rock being subordinate members), as applicable to all the higher portion of this [Grauwacke] series which has a tripartite character in Salop and Hereford, due to the interpolation of the Wenlock and Aymestrey Limestone" (p. 477).

This initial confusion of the limestones was quickly resolved by Murchison (1834) who produced a "Table of the stratified Deposits beneath the Coal measures" covering much of the Welsh Borderland and South Wales, and giving the thickness, lithological characters, characteristic organic remains and main localities of each of

the formations. Part of this table shows :

Old Red Sandstone		c. Tilestone
Upper Grauwacke Series	I. Ludlow rocks	d. Upper Ludlow rock
		e. Aymestry and Sedgeley limestone
		f. Lower Ludlow rock
	II. Wenlock and Dudley rocks	g. Wenlock and Dudley limestone
		h. Wenlock and Dudley shale

Here the two limestones were recognized as being of different ages and the name "Aymestry", with the second "e" omitted, was applied to the higher one.

Murchison (1835 : 46) made the first reference to the "Silurian System of Rocks". The publication in 1839 of his "Silurian System" provided the first detailed account of these rocks and of the Ludlow district and figured the organic remains by which the subdivisions were to be recognized. No precise limits to the system were defined, but Murchison's references (pp. 181, 198) to the "Downton Castle building stone" as "constituting the upper stratum of the Silurian System, and the 'bone bed' as the central part of the Fish bed (8 to 10 ft. thick) beneath the Downton Castle building stone", certainly make it clear that he did not use the Ludlow Bone Bed as a limit of either the Ludlow Rock or the Silurian System, and that the upper limit of the latter was placed at the top of the building stone (12 to 14 ft. thick). He appears, therefore, to have regarded the upper limit of the Ludlow Rock as some 16 to 19 ft. above the Ludlow Bone Bed, but was clearly aware of the transitional nature of the junction. A similar account of the district was given in Murchison's shorter work "Siluria", first published in 1854.

Murchison (1857 : 290) stated that "the Tilestones of Shropshire and Herefordshire which connect the Silurian and Devonian rocks may, according to the predominance of certain fossils, be classed either with the inferior or the superior system. Their maximum thickness may be considered to be about 40 or 50 ft."

Shorter contributions on various aspects of the geology of the Ludlow area were made by Murchison (1853), Egerton (1857), Harley (1861), Curley (1863), Lightbody (1863, 1869), Brodie (1869) and Marston (1870).

Wood (1900) established graptolite zones for the Lower Ludlow and discussed the lower and upper limits of Murchison's Lower Ludlow Formation. Whilst pointing out (p. 42) that Murchison drew the base of the Ludlovian "at the Wenlock Limestone", she put forward the view reached jointly with Elles, that the base of the zone of *Monograptus vulgaris* should be regarded as the Wenlock-Ludlow boundary. As indicated on her Table I, this zone at Ludlow lacks graptolites.

Elles & Slater (1906) classified the highest Silurian rocks of the Ludlow district into :

- I. Temeside Group
- II. Upper Ludlow Group
- III. Aymestry Group

and erected a zonal scheme based on brachiopod species. The Ludlow Bone Bed

was included at the top of II and the Downton Castle Sandstones (see p. 199) "used practically in the same sense as Murchison's Downton Castle Building Stone", were grouped together with the succeeding Temeside Shales in III, which were regarded as passage beds into the Old Red Sandstone. One effect of this was to place the Silurian-Devonian boundary at the top of the Temeside Shales, about 170 ft above the Ludlow Bone Bed. The area mapped extended from Mocktree Hill to Caynham, but outcrops of formations older than the Aymestry (*Conchidium*) Limestone were omitted.

Alexander (1936) made a study of the Aymestry Limestone of the main outcrop, described its lithology and fauna, and gave an interpretation of the conditions of its deposition. Her table of succession (p. 104) placed the Aymestry Limestone in the zone of *Monograptus leintwardinensis*, but with its base descending in many places into the zone of *Monograptus tumescens*. The *Dayia navicula* beds were shown to rest unconformably on the eroded surface of the Aymestry Limestone. The area mapped extended from Craven Arms, across the Ludlow Anticline to Aymestrey. Outcrops of formations from the Wenlock Limestone to the Lower Whitcliffe (*Rhynchonella nucula*) Beds were shown.

Straw (1927) recorded fish remains from below the Ludlow Bone Bed (Whitcliffe Flags). White (1950 : 58-65) in an analysis of the "vexed question of the Silurian-Old Red boundary", supported the claims of the law of priority "having regard to the demands of practicability", and therefore suggested the slight adjustment involved in accepting the Ludlow Bone Bed as the "datum line from which to mark the boundary in other areas".

The area here described differs somewhat from that covered by Elles & Slater (1906). It extends from the River Teme at Downton Gorge (adjoining the Leintwardine area recently described by Whitaker, 1962), eastwards to Ludlow and then southwards to Richards Castle (adjoining the area mapped by B. J. Williams).

Earlier papers dealt with varying portions of the stratigraphical sequence. The present paper describes the succession from the Wenlock Shales to the base of the Ludlow Bone Bed, here regarded (following White, 1950) as the base of the Old Red Sandstone. Downtonian outcrops are shown on the map only as bounding the area to the north and east.

II. STRATIGRAPHICAL CLASSIFICATION

In erecting a stratigraphical classification for the Ludlow district an attempt has been made to follow the recommendations of the American Commission on Stratigraphic Nomenclature (1961). The particular characteristics of the succession in the Ludlovian rocks of the Welsh Borderland seem to require some modification of the recommended usage.

According to the American Commission the three main categories of stratigraphical divisions are rock-stratigraphical units, biostratigraphical units, and time-stratigraphical units. The divisions in the Ludlow district have been mapped mainly on the basis of their faunal assemblages but lithological characteristics have also proved very helpful in their identification. These units are therefore biostratigraphical and to a lesser extent rock-stratigraphical. If the recommended practice for the

TABLE I.—*Silurian Succession of Ludlow District*

Series	Stage	Local division	Thickness in feet (approx.)	Lithology	Earlier classification
LUDLOVIAN (approximately 1,000 to 1,300 ft.)	WHIT-CLIFFIAN	Upper Whitcliffe Beds	100	Flaggy calcareous siltstones with shelly limestone bands	Upper Whitcliffe or <i>Chonetes</i> Flags
		Lower Whitcliffe Beds	80	Irregularly bedded, massive or thickly flaggy calcareous siltstones	Lower Whitcliffe or <i>Rhynchonella</i> Flags
	LEINTWARDINIAN	Upper Leintwardine Beds	5 to 18 (thicker eastwards)	Flaggy calcareous siltstones	-----
		Lower Leintwardine Beds	100	Thinly flaggy calcareous siltstones	Mocktree or <i>Davia</i> Shales
	BRINGEWOODIAN	Upper Bringewood Beds	40 to 150 (thinner eastwards)	Irregularly flaggy or nodular silty limestones	Aymestry or <i>Conchidium</i> Limestone
		Lower Bringewood Beds	160 to 200 (thicker eastwards)	Flaggy calcareous siltstones with limestone nodules	
	ELTONIAN	Upper Elton Beds	150 to 250	Well bedded, flaggy calcareous siltstones with flaggy limestone bands	Lower Ludlow Shales
		Middle Elton Beds	150 to 350 (thinner eastwards)	Conchoidally fracturing, shaly and thinly flaggy, muddy siltstones	
		Lower Elton Beds	100 to 150	Irregularly bedded, shaly and flaggy, calcareous silty mudstones	
WENLOCKIAN	Wenlock Limestone	Wenlock Limestone	200 to 450 (thinner eastwards)	Flaggy silty limestones alternating with calcareous silty shales, 50-60 ft. of nodular limestone at top	Wenlock Limestone
		Wenlock Shales	approx. 1,000 seen	Thinly flaggy, calcareous silty mudstones or calcareous silty shales	Wenlock Shales

former category of unit were observed, they would be called assemblage zones and named after one or more of the characteristic fossils, even though these fossils are not confined to the zone. This would be practicable, although unsatisfactory, for some of the Ludlovian divisions; but in others no single fossil is sufficiently characteristic or restricted to serve as a label for the whole division. Moreover the taxonomic revision of a fossil name which has been used in this way is liable to cause confusion. This practice may also result in the same fossil name being used in different areas for units which are not even homotaxial. For instance, a study of their complete faunal assemblages indicates that the *Wilsonia* Shales of Builth and the *Wilsonia wilsoni* Grits of Kerry are not biostratigraphical equivalents. To add to the confusion the index fossil is now renamed *Sphaerirhynchia wilsoni* and accordingly the Stratigraphical Code would require the renaming of the unit. In the Ludlow district, in particular, this scheme would result in the resurrection of such names as the *Conchidium knighti* Zone and the *Dayia navicula* Zone, both of which have given rise to confusion. An alternative in this instance would be to call the assemblage zones after localities (e.g. the Bringewood Zone), but this would fail to express the fact that the divisions are partly rock-stratigraphical units. The use of the term "Formation" is intended only for units which are defined essentially on their lithological characteristics. All these considerations seem to justify the use of the non-committal term "Beds" in naming the stratigraphical divisions in the Ludlow district.

This new classification does not render all the more familiar names obsolete but it is necessary to realize their limitations. The term Aymestry Limestone, for instance, refers to a rock-stratigraphical unit. It has been used, and can continue to be used, for the limestone development in the middle of the Ludlovian, even though this limestone is in the Upper Bringewood Beds at Aymestry and View Edge but in the Lower Leintwardine Beds along Wenlock Edge. Ideally, perhaps, the name Aymestry Limestone should be used only if lithological continuity with the limestone of the type area is proved, but it has also been applied, not unreasonably, to the calcareous developments in a similar stratigraphical position at Usk, Woolhope and Malvern. It cannot logically be applied, however, if the unit passes laterally into strata which are not sufficiently calcareous to justify the use of the term limestone; this problem arises in the Usk inlier (see p. 148) and to the west of Aymestry. It should also be remembered that the limestones of the Ludlovian are rarely very pure so that differences of opinion may easily arise as to whether the beds are sufficiently calcareous to justify the term limestone.

Biostratigraphical divisions are usually of more widespread validity than rock-stratigraphical units, particularly if the diagnostic fossils are independent of facies changes. They are also less likely to be diachronic if the characteristic fossils are carefully chosen; it is very important, however, not to regard faunal units as *necessarily* of time significance merely because more refined criteria are not yet available. In the present mainly biostratigraphical classification the pattern of faunal changes (Text-fig. 1) is strictly applicable only to the shelf region but within that region it facilitates correlation across differing facies. For instance, the Lower Leintwardine Beds near Leintwardine and Downton have previously been called

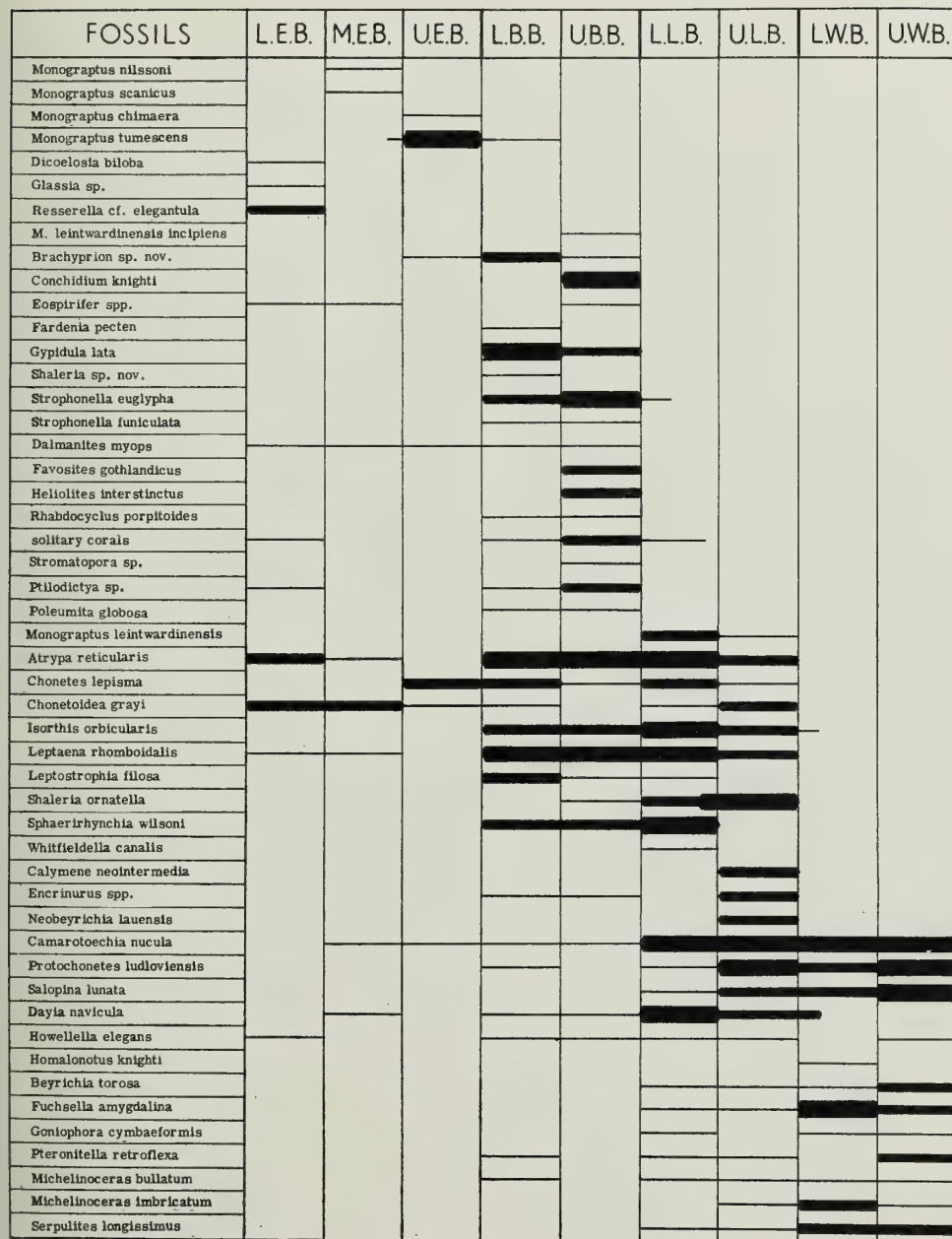


FIG. 1. Range chart of selected Ludlovian fossils. Thin lines indicate "present", medium lines "fairly common" and thick lines "common".

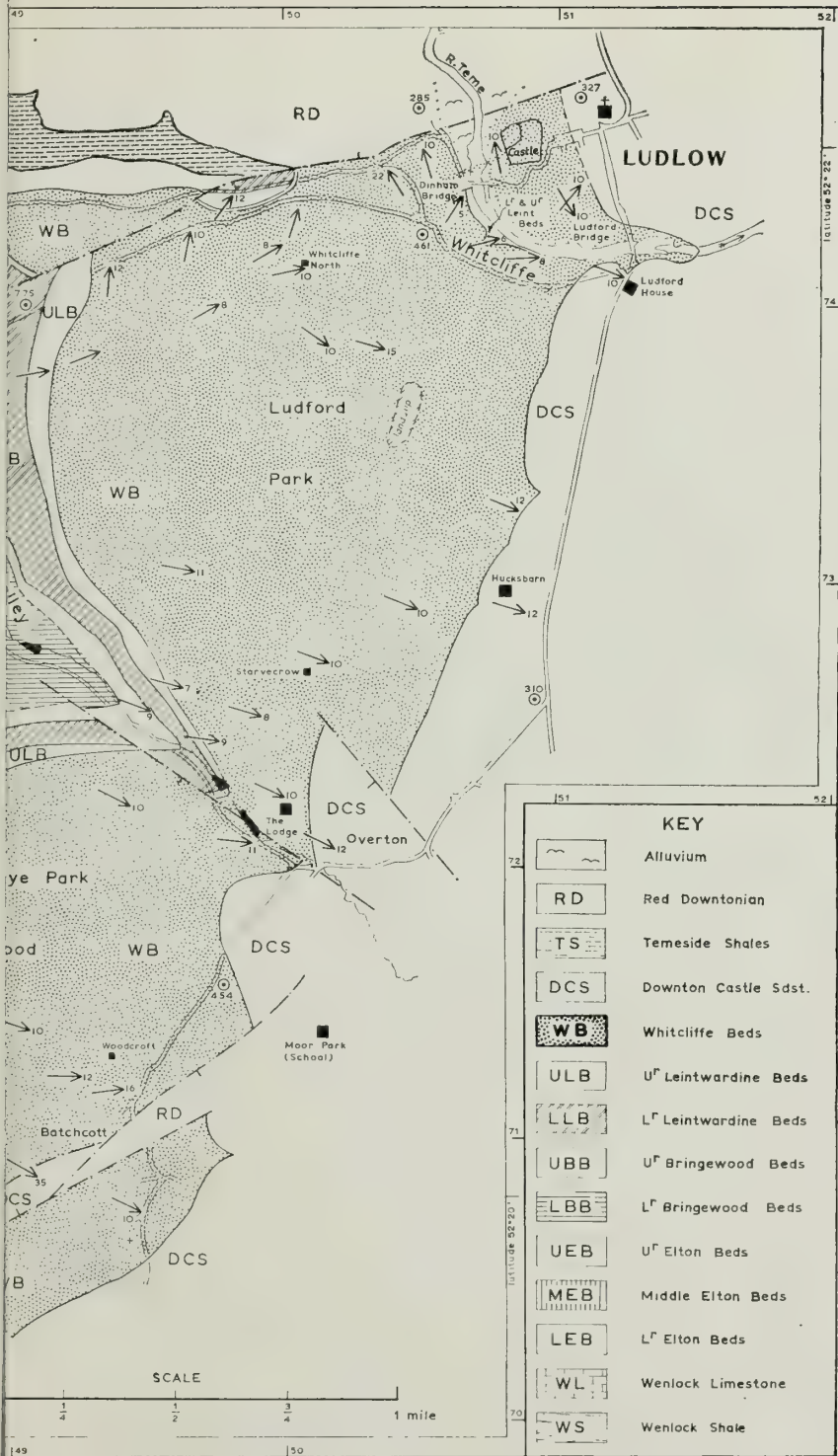
(using a rock-stratigraphical term) Mocktree Shales, whereas strata with a similar faunal assemblage have been called Aymestry Limestone near Ludlow and along Wenlock Edge. Equivalent beds in the basin region are not referred to as Lower Leintwardine Beds because their faunal assemblage is very different from that determined at the standard section. A fairly certain correlation can nevertheless be made based partly on the occurrence of *Monograptus leintwardinensis* and partly on a study of transitional faunas in intermediate areas.

The facies and faunal changes in the basin region are more complex than those on the shelf and in order to simplify the picture a compromise between a rock-stratigraphical and a biostratigraphical classification has again had to be devised (see Table II). Otherwise, most of the present local classifications would have to be used in general discussions on the basin region.

The biostratigraphical divisions of this revised classification for the Ludlow area are here defined at standard localities, the position of each boundary being indicated on a sketch-map or section (except in the case of that between the Lower and Upper Bringewood Beds where this is not necessary). Each boundary is defined by the basal surface of a particular bed and *not* at the parting between beds. Should it be proved at some later time that this parting represents a significant break in deposition at the standard locality any sediments deposited elsewhere during the time represented by this gap will automatically be grouped in the lower unit and will not necessitate the institution of a new division. Although there are distinct faunal and lithological changes at most of the junctions no signs of important breaks have been detected. The bases of the Lower Elton Beds, Lower Bringewood Beds, Lower Leintwardine Beds, and Lower Whitcliffe Beds have been selected as bases of stages.

Even though a refined system of absolute dating is as yet unattained, the stratigrapher must continually be concerned about the *relative* dating of geological events. The ideal correlation is a time correlation. For this purpose a scale of time-stratigraphical units has been evolved, but the smaller these units are, the more difficult is their world-wide recognition. Ideally, there should be only one set of time-stratigraphical units. This ideal is almost realized for the systems but different sets of series tend to be erected for each major region such as a continent. Stages are even more numerous and cover smaller regions; they are justifiable as a temporary expedient if they link together a variety of local successions into a time-stratigraphical scheme which cannot as yet be linked to the master set of stages in the type area.

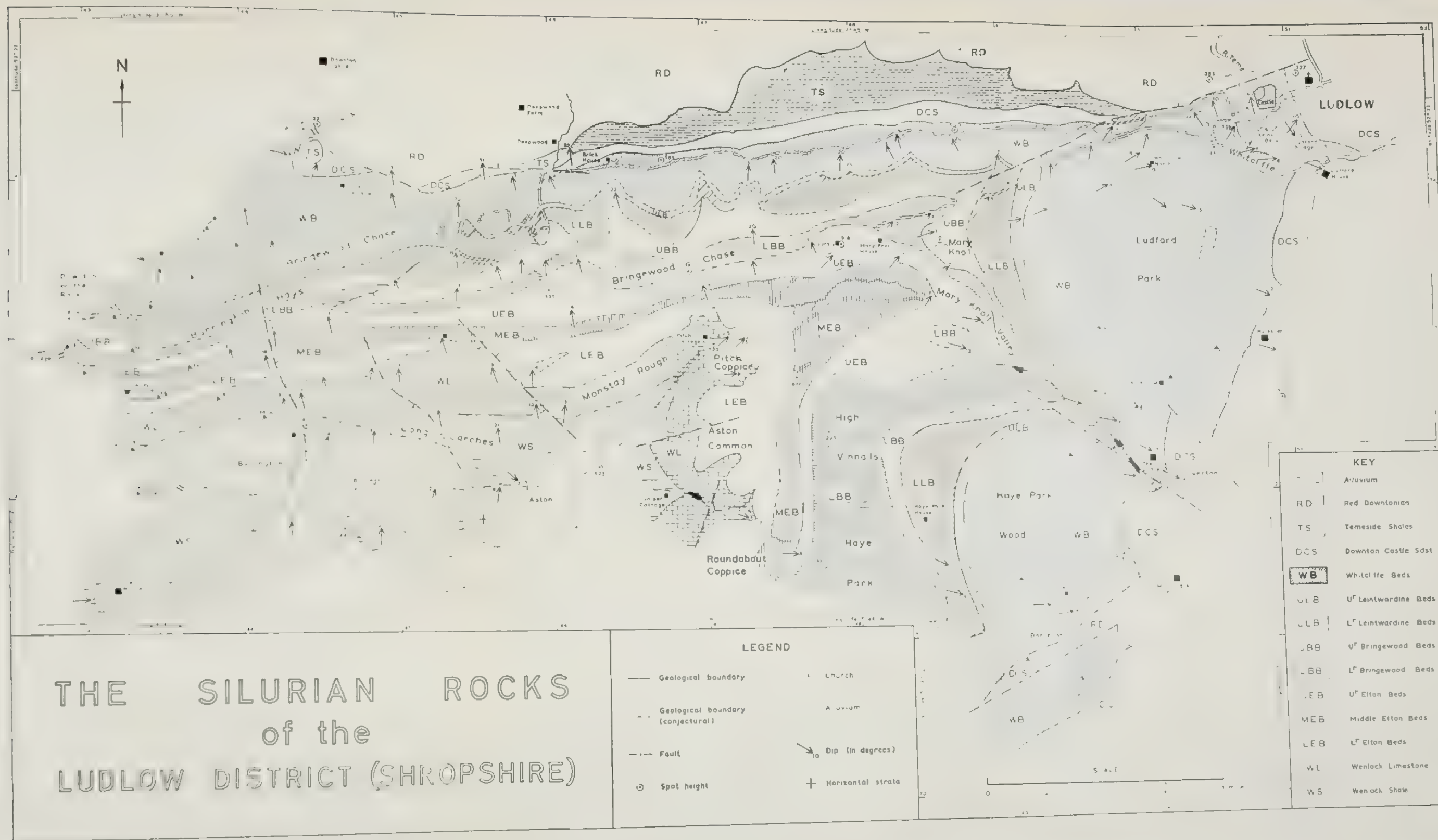
As Ludlow is the type area for the Ludlovian Series, the institution of stages needs no further justification, for they become a necessary part of the reference scale of time-stratigraphical units for the whole world. In addition, however, these four stages are needed for linking together the very varied successions in the Ludlovian of the British Isles when discussing palaeogeography, palaeoecology, etc. The only terms hitherto available have been terms such as Lower Ludlovian, Middle Ludlovian, and Upper Ludlovian, which have been used with a confusing variety of meaning. It is here recommended that these terms be abandoned in favour of the fourfold stage classification.



THE SILURIAN ROCKS of the LUDLOW DISTRICT (SHROPSHIRE)

LEGEND	
— Geological boundary	• Church
- - - Geological boundary (conjectural)	▲ Aulium
- - - Fault	↘ Dip (in degrees)
① Spot height	+ Horizontal strata

KEY	
RD	Red Devonian
TS	Temside Shales
DCS	Downton Castle Sdst
WB	Whitcliffe Beds
ULB	U ^r Leintwardine Beds
LLB	L ^r Leintwardine Beds
UBB	U ^r Bringewood Beds
LBB	L ^r Bringewood Beds
UEB	U ^r Elton Beds
MEB	Middle Elton Beds
LEB	L ^r Elton Beds
WL	Wenlock Limestone
WS	Wenlock Shale



The stage boundaries have been chosen to coincide with the boundaries of the major biostratigraphical units at the standard sections. Ideally a time-stratigraphical junction should be in a sequence devoid of sudden faunal and lithological changes but the contrasts in this Ludlovian succession are certainly not dramatic enough to justify a separate set of stage boundaries with separate names. Ideally again, the names of the stages should be different from those of the biostratigraphical divisions even though the boundaries are the same, for if it is later proved that the base of, say, the Lower Leintwardine Beds is diachronic they may then be partly of Bringewoodian age and not Leintwardinian. Such a contingency does not seem sufficiently likely to justify the use of separate names for the stages.

The standard sections for the bases of the biostratigraphical divisions are described in Section III unless they are also standard sections for stages in which case they are described in Section VI.

III. DETAILED ACCOUNT OF THE SUCCESSION

In this section the stratigraphical divisions are described in turn. A brief mention of the topographical expression of each, where necessary, is followed by detailed descriptions of lithology and fauna. Then, where applicable, a standard section is described. Finally a list of good exposures is given. Symbols corresponding to the colour terms used in the lithological descriptions have been left out of this section and are listed in Appendix 2, where also is given a list of carbonate determinations for selected samples of the beds. The pattern of faunal changes within the Ludlovian is expressed in the faunal range chart (Text-fig. 1).

In the illustrations of this paper and in the List of Localities (Appendix 1) the following symbols have been used to represent the various stratigraphical divisions :

R.D.	Red Downtonian	L.L.B.	Lower Leintwardine Beds
T.S.	Temeside Shales	U.B.B.	Upper Bringewood Beds
D.C.S.	Downton Castle Sandstone	L.B.B.	Lower Bringewood Beds
B.B.	Ludlow Bone Bed	U.E.B.	Upper Elton Beds
W.B.	Whitcliffe Beds (undifferentiated)	M.E.B.	Middle Elton Beds
U.W.B.	Upper Whitcliffe Beds	L.E.B.	Lower Elton Beds
L.W.B.	Lower Whitcliffe Beds	W.L.	Wenlock Limestone
U.L.B.	Upper Leintwardine Beds	W.S.	Wenlock Shales

(a) *Wenlock Shales*

The outcrop of the Wenlock Shales forms a triangular area of low-lying and predominantly pastoral land in the denuded core of the plunging anticline. It is poorly exposed, except near Burrington and is much covered by alluvium. These beds, at least 1,000 ft. thick, are soft, light olive grey to pale olive, calcareous, thinly flaggy silty mudstones or silty shales, with irregular and infrequent seams of fine-grained nodular limestone. The beds may appear massive to thickly flaggy in fresh exposures, where a large-scale conchoidal fracture is seen. Weathering accentuates the fundamental thinly flaggy or shaly bedding, together with a smaller scale conchoidal fracture and blocky jointing. It also produces colour changes to yellowish

grey, dark yellowish orange, or brownish grey, of which the last is seen especially on joint and fracture faces. Characteristically, weathering produces a light-coloured dusty appearance.

Owing mainly to lack of exposures the Wenlock Shale fauna has not been studied in detail. Small brachiopods and trilobites are the commonest fossils but the numerous shell fragments are not easily identifiable. The more important fossils are as follows :

Dalmanites myops (fairly common)

Chonetoides grayi

Cyrtia exporrecta

Dicoelosia biloba

Dolerorthis rustica

Calymene sp.

Dalmanites caudatus

Phacops sp.

Hemsiella maccoyana

solitary corals

Dawsonoceras annulatum

Monograptus dubius

— *vulgaris*

Gothograptus nassa

SELECTED LOCALITIES

Locality 40 : see Section IV (d) page 133

Locality 38 : see Section IV (d) page 133

Locality 61 : see Section IV (d) page 136

Locality 100 : see Appendix 1 page 164

Locality 114 : see Appendix 1 page 165

Locality 141 : see Appendix 1 page 166

(b) *Wenlock Limestone*

The Wenlock Limestone forms wooded scarps which are in places offset along fault-lines. It thins eastwards from 450 to 200 ft. Its base is marked by the relatively sudden occurrence of numerous ribs of hard, irregularly bedded, light olive grey to pale olive, silty limestone, alternating with beds similar to the bulk of the Wenlock Shales. These ribs, which are irregularly and infrequently developed in the Wenlock Shales, form 40% or more of the succession in the Wenlock Limestone, protruding conspicuously in exposures. They weather to a yellowish grey colour or sometimes to the condition of brown rottenstones. In some cases it is evident that the hard ribs represent the coalescence of limestone nodules.

The above description applies to the greater part of the Wenlock Limestone of the district, but the uppermost 50 ft. or so of the formation is predominantly hard nodular limestone. The individual nodules (2 to 8 in. long) are arranged in flaggy units ; they are medium grey when fresh but weather to a yellowish grey. The nodular effect is accentuated by weathering, with the development of softer, dusty looking, surrounds to the nodules ("lenticular" texture of Hadding, 1958).

The limestone is finely crystalline (crystals often about 0.05 mm.) but impure, or may have an obviously important organic content of, for example, of brachiopods, bryozoa, or crinoid fragments. The aggregates of anhedral crystals of calcite in the crystalline limestones are presumably themselves diagenetically recrystallized organic fragments. Bands and concentrations of particular fossils may occur, for example

a band of the coral *Entelophyllum articulatum* at Locality 111. Some *Favosites* and stromatoporoid colonies reach a substantial size; an example of the latter, in position of growth (Locality 65) is 14 in. in diameter and 5 in. in height.

In addition to the dominant nodular limestones there are partings of shaly or irregularly flaggy, silty limestones, light olive grey to pale olive in colour.

Compared with the well-known outcrops on Wenlock Edge and at Dudley, the Wenlock Limestone of the Ludlow area is not very fossiliferous; the corals occur mainly in the more calcareous nodular beds at the top. In the lower flaggy division the most important fossils are as follows:

Atrypa reticularis

Dolerorthis rustica

Eospirifer radiatus

Sowerbyella sp.

Sphaerirhynchia wilsoni

bryozoa

From the nodular division the main elements of the fauna are :

Favosites spp. (fairly common)

Heliolites interstinctus (fairly common)

Thecia grayana

Entelophyllum articulatum

solitary corals

Stromatopora carteri

Atrypa reticularis (fairly common)

Gypidula galeata

Leptaena rhomboidalis (fairly common)

Resserella elegantula

Rhipidomella hybrida

Sphaerirhynchia wilsoni

Strophonella euglypha

Calymene sp.

Dalmanites myops

Poleumita discors

crinoid columnals (common)

SELECTED LOCALITIES

Locality 63 : see Section IV (d) page 136 (lower flaggy limestones)

Locality 65 : see Section IV (d) page 136 (upper nodular limestones)

Locality r4 : see Section IV (b) page r28 (flaggy)

Locality 16 : see Section IV (b) page 128 and Section VI page 130

(upper nodular Wenlock Limestone succeeded by Lower Elton Beds; this is the standard section for the base of the Eltonian).

Locality 140 : see Appendix 1 page 166 (flaggy limestones)

Locality 163 : see Appendix 1 page 166 (nodular)

(c) *Lower Elton Beds*

The softer Lower Elton Beds have been eroded from the underlying Wenlock Limestone to form a step feature or valley, usually unforested. They are approximately 100 to 150 ft. thick and poorly exposed. In sharp contrast to the upper Wenlock Limestone they are soft, pale olive, calcareous, finely micaceous, silty mudstones or muddy siltstones, irregularly bedded in shaly or flaggy units and with a somewhat blocky fracture. They weather towards a dark yellowish brown, but a "greenish" colour speckled white with shell fragments is also characteristic of the beds. The shell fragments are sometimes tightly packed, one within the other. Fresher exposures may appear thickly flaggy, weathering to a more thinly bedded

appearance as well as to a light dusty effect, reminiscent of the Wenlock Shales. In addition to the mudstones and siltstones there are greenish-grey, egg-shaped nodules, rounded slabs and discontinuous bands of hard compact limestone, which tend to be more conspicuous in the lower part of the division.

The Lower Elton Beds are characterized by a shelly fauna of Wenlockian affinities in which small brachiopods and trilobites predominate.

Common or fairly common fossils :

Resserella cf. *elegantula* (not found above these beds)

Atrypa reticularis

Chonetoides grayi

Less common but important fossils :

Dicoelosia biloba (not found above these beds)

Gypidula galeata

Plectatrypa imbricata } (not found above these beds)

Chonetes minimus

Eospirifer plicatellus

Glassia sp.

Howellella elegans

Leptaena rhomboidalis

Dalmanites myops

Hemsiella maccoyana

Halysites catenularius

Alexander (1936) called these "Barren" beds but only because of the absence of graptolites; small shells and shell fragments are usually abundant although not easily identifiable. Paucity of exposures has resulted in a rather incomplete and possibly unrepresentative faunal list. In adjacent areas and the south-eastern inliers all the species listed as belonging to the Elton Bed fauna (Lawson, 1960 : 116) may occur in these beds.

The standard section for the base of the Lower Elton Beds, which is also that for the base of the Ludlovian Series and the base of the Eltonian Stage, is described in Section VII on pages 139-141.

SELECTED LOCALITIES

Locality 73 : see Section IV (d) page 136

Locality 70 : see Section IV (d) page 136

Locality 69 : see Section IV (d) page 136 and Section III page 107

(Lower Elton Beds succeeded by Middle Elton Beds; this is the standard locality for the base of the Middle Elton Beds).

Locality 101 : see Appendix 1 page 164

Locality 162 : see Appendix 1 page 166 (base of Lower Elton Beds)

(d) Middle Elton Beds

Outcrops of the Middle Elton Beds, which are poorly exposed, form the foot of the

wooded scarps of Bringewood Chase and High Vinnalls. These beds thin appreciably eastwards from approximately 350 to 150 ft. They are well bedded, light olive grey, shaly or thinly flaggy siltstones, with a characteristic, smooth, conchoidal fracture and "soapiness" to the touch. The weathered appearance is yellowish grey with, less commonly, a white dustiness. The well defined bedding planes, paucity of lime, and marked colour changes make these beds clearly distinguishable from the Lower Elton Beds, the transition taking place within a few feet. Less common in the Middle Elton Beds are slightly calcareous, muddy siltstones with some finely divided mica. Occasionally there are papery shales and calcareous nodules. Crinkle marks (Williams & Prentice, 1958) occur rarely and one specimen from these beds (Locality 42) shows a concentration of broken orthoconic nautiloids.

The Middle Elton Beds show a sharp faunal change from the Lower Elton Beds; benthonic forms are rare and graptolites and orthoconic nautiloids predominate.

Common or fairly common fossils :

Monograptus colonus
Chonetoides grayi
Hemsiella maccoyana
 orthoconic nautiloids

Less common but important fossils :

Dayia navicula (not found below these beds)

Lingula lata

Dalmanites myops

Slava interrupta

Monograptus comis

—— *dubius*

—— *nilssoni*

—— *scanicus*

—— *uncinatus* var. *orbatus*

—— *varians*

—— *tumescens* (in highest beds only)

} (apparently restricted to these beds)

These are the Lower Ludlow Shales of the *Monograptus nilssoni* and *M. scanicus* zones of Wood (1900).

The standard section for the base of the Middle Elton Beds is along the stream named Nunfield Gutter (referred to on pages 133 and 136), which flows westwards to join the River Teme near Owney Cottage. This section, about 710 yards east-north-east of Owney Cottage, is on a southward bend in the stream (43897278). Its position is indicated as Locality 69 in the sketch-map (Text-fig. 10) and a detailed plan of the exposures is given in Text-fig. 2. As shown in the latter the boundary follows the stream obliquely across the southern part of the bend and there are exposures in the southern bank which give continuous sections across it. The scale in Text-fig. 2 relates to measurements along the stream. The exposures themselves are shown somewhat diagrammatically.

The lithological change from Lower to Middle Elton Beds is a relatively sharp

one, the transition taking place in about 3 ft. of strata. The irregularly bedded, slightly more thickly flaggy, calcareous siltstones of the Lower Elton Beds, with some limestone nodules, are succeeded by more thinly and better bedded siltstones of the Middle Elton Beds. The change may be seen in the exposures along the stream bank at either A to C or D to E.

The Lower Elton Beds are rich in shelly fossils, though these are often fragmentary. The following were collected from the stream bank at A: *Atrypa reti-*

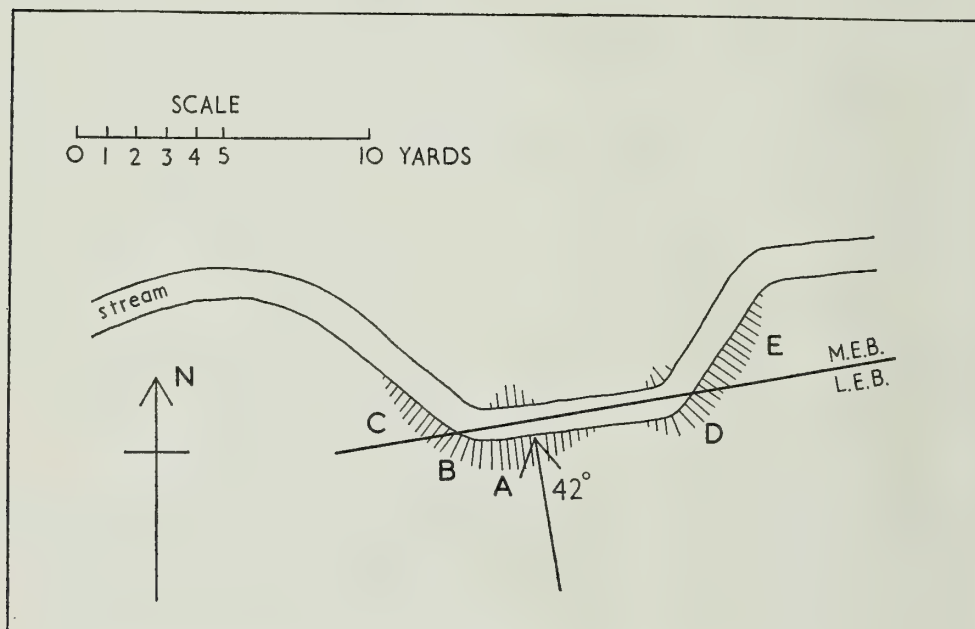


FIG. 2. Plan of the standard locality in Nunfield Gutter for the boundary between the Lower Elton Beds and the Middle Elton Beds (for explanation see p. 107).

cularis, *Chonetoides grayi*, *Dicoelosia biloba*, *Glassia* sp., *Howellella elegans*, *Leptaena rhomboidalis*, *Nuculites* sp., *Pterinea* sp., *Dalmanites myops* and a graptolite fragment. Higher in the stream bank at A is a thin, brown weathering, clay band which may be traced also at the eastern end of the exposure between D and E. The beds (B) up to 13 in. above the clay band yielded graptolite fragments together with *Chonetoides grayi*, *Dicoelosia biloba*, *Glassia* sp., an undetermined lamellibranch, *Michelinoceras* sp., *Dalmanites myops*, a proetid pygidium and an ostracod. The association of more abundant graptolite fragments and fewer shelly fossils, together with the presence of *Dicoelosia biloba* suggests that this is a transitional fauna at the top of the Lower Elton Beds. The base of the Middle Elton Beds has been taken at an horizon 18 in. above the top of the clay band. Above this (C) graptolite fragments, including *Monograptus uncinatus* var. *orbatus*?, are associated with *Chonetoides grayi* and *Michelinoceras* sp. About 2 ft. above the boundary the typically thinner and smoother bedding of the Middle Elton Beds is developed.

The graptolites collected from these typical Middle Elton Beds include *Monograptus nilssoni* and *M. uncinatus* var. *orbatus*.

SELECTED LOCALITIES

Locality 75 : see Section IV (d) page 136

Locality 72 : see Section IV (d) page 136

Locality 69 : see Section IV (d) page 136 and Section III page 107

(Middle Elton Beds succeeding Lower Elton Beds ; this is the standard locality for the base of the Middle Elton Beds)

Locality 17 : see Section IV (b) page 128

(e) *Upper Elton Beds*

The Upper Elton Beds near Downton Gorge form a subsidiary feature. Farther east they rise to form the westernmost of the three summits (over 1,200 ft. O.D.) of Bringewood Chase. Elsewhere their outcrop makes a steep wooded slope. The Upper Elton Beds vary in thickness from approximately 150 to 250 ft. In the uppermost part of the Middle Elton Beds the shaly and thinly flaggy siltstones become somewhat harder and calcareous. At the base of the Upper Elton Beds conspicuous ribs of hard, more calcareous siltstone appear and soon become the typical lithology. This typical sediment of the Upper Elton Beds is a well bedded, compact, light olive grey, flaggy, calcareous, coarse siltstone (here, as in all the other Ludlovian siltstones in the succession, the silty material is largely of angular quartz). Shaly and thinly flaggy siltstones are rarer, as are nodular or flaggy limestone bands. The bedding surfaces are characteristically smooth or only slightly irregular. They give a "ringing" effect under the hammer and it is often possible to break off large sheets of rock. There is some lamination shown by slight changes of grain size and layers of greater concentration of dark material together with the angular quartz grains. Weathering reduces the rock first to a yellowish grey and then to dark yellowish-brown. Graptolites and orthoconic nautiloids tend to occur in concentrated patches on certain bedding planes.

Sedimentary structures of various kinds are frequent in the Upper Elton Beds. Both current bedding and slump structures occur and crinkle marks are very common. It is difficult to find accurately orientated specimens as the best exposures are on steep slopes or faces on which slipping has taken place. The few orientated specimens which have been collected from exposures near the River Teme (Locality 43) do not always show a clear overturning of the crinkled laminae. Such measurements as have been made suggest a movement in a south-south-easterly direction, which is directly opposed to that deduced by Williams & Prentice (1958) from exposures in the southern limb of the Ludlow Anticline at the same stratigraphical horizon.

Although the Upper Elton Beds are predominantly graptolitic the varied fauna of the Middle Elton Beds has disappeared and *Monograptus tumescens* is the only common graptolite.

Common or fairly common fossils :

Monograptus tumescens

Chonetes lepisma (locally fairly common)

orthoconic nautiloids

Less common but important fossils :

Brachyprion sp. nov.

Chonetoides grayi

Lingula lata

Dalmanites myops

Monograptus chimaera

These are the Lower Ludlow Shales of the zone of *Monograptus tumescens* as described by Wood (1900).

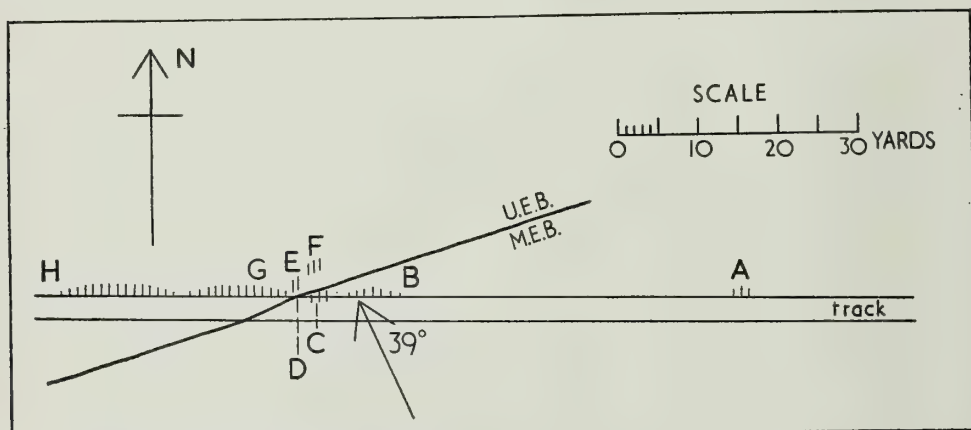


FIG. 3. Plan of the standard locality near Owney Wood for the boundary between the Middle Elton Beds and the Upper Elton Beds (for explanation see below).

The standard locality for the base of the Upper Elton Beds is along the north side of the track which climbs obliquely across the lower part of the scarp north-east of Owney Wood. The grid reference is 43677283 and its position is shown as Locality 76 in Text-fig. 10. A detailed plan of the exposures along the track is given in Text-fig. 3. Point D, where the base of the Upper Elton Beds crosses the north margin of the track, lies 239 yards from the gate post (43887280) at the foot of the track, and 238 yards from the gateway (43527284) at the top where the track enters the upper part of Owney Wood.

Though the Middle and Upper Elton Beds have different graptolite faunas they are most easily distinguished in the field by their characteristic lithologies. In this section, which is one of the few in which strata close to the boundary are exposed, a lithological transition is seen between the two divisions. The base of the Upper Elton Beds has been taken near the first of the hard calcareous flaggy ribs which characterize these beds.

Details of the section are as follows: ascending the track from the gatepost previously mentioned, the first exposures occur after 183 yards at point A, where fairly typical Middle Elton Beds are seen. These are relatively soft, mostly shaly

siltstones (not calcareous) showing characteristic conchoidal fracture and weathering to a slightly yellowish colour. *Monograptus varians* was collected here, together with *Chonetoides grayi* and *Michelinoceras* sp.

The beds exposed at point B, though still mostly shaly, are harder than typical Middle Elton Beds and slightly calcareous. *Monograptus tumescens* was collected here so that, in this section at least, this graptolite appears before the typical lithology of the Upper Elton Beds. Also present are *Kionoceras angulatum* and *Michelinoceras* spp. At point C, immediately below the chosen boundary, the same lithology is maintained. *Michelinoceras* sp. is present together with fragments of graptolites and shelly fossils.

At point E the hard shaly and thinly flaggy siltstones are associated with the first prominent flaggy ribs of very hard calcareous siltstone. The base of the Upper Elton Beds has therefore been taken between C and E (i.e. at point D). *Monograptus tumescens* was collected from E. Similar beds at about the same horizon are poorly exposed at point F, in the north-western corner of an overgrown excavation a few yards north of the track. At point G, along the track again and farther west, *M. tumescens*, associated with *Chonetoides grayi* was again collected. Flaggy ribs are more common here and at the western end of the exposures (point H) are sufficiently prominent for the lithology to be recognized as fairly typical of the Upper Elton Beds. *M. tumescens* is common here and a pygidium of *Dalmanites myops* has been collected.

SELECTED LOCALITIES

Locality 43 : see Section IV (d) page 133

Locality 107 : see Appendix 1 page 165

Locality 18 : see Section IV (b) page 128

Locality 170 : see Appendix 1 page 167

Locality 164 : see Appendix 1 page 166

Locality 165 : see Appendix 1 page 166

(f) *Lower Bringewood Beds*

The crest of the Ludlovian scarp feature of High Vinnalls and the eastern summits of Bringewood Chase are formed by Lower Bringewood Beds which also extend in places some way down the dip slope. These beds thicken slightly eastwards, from approximately 160 to 200 ft. Their base is marked by the appearance of many bands of shelly fossils, by more frequent bands and lenses of silty limestone, and by the development of calcareous siltstones somewhat thicker and more irregularly bedded than those of the Upper Elton Beds, which they quickly replace. These irregularly bedded, calcareous, finely micaceous, medium-coarse siltstones are light olive grey in colour, sometimes weathering to pale olive. Some of the more calcareous siltstones are medium grey when fresh, but weather to a brown rottenstone, as do some of the shelly limestone bands.

The Lower Bringewood Beds show a marked faunal contrast to the Upper Elton Beds; graptolites and orthoconic nautiloids are rare, whereas large brachiopods (particularly strophomenids) are abundant. In the Ludlow area the faunal change is accentuated

because of this change from a graptolitic to a shelly facies, but even in those areas where the equivalents of the Elton Beds have a more benthonic fauna the change is distinct. The disappearing Elton Bed fauna has been listed by Lawson (1960 : 116). Most of the typical Bringewood Bed fossils are familiar Wenlockian species returning with the change to shallow water and calcareous conditions.

Common or fairly common fossils :

<i>Brachyprion</i> sp. nov.	} (Less common in Upper Bringewood Beds)
<i>Leptostrophia filosa</i>	
<i>Dalmanites myops</i>	
<i>Atrypa reticularis</i>	
<i>Chonetes lepisma</i>	
<i>Gypidula lata</i>	
<i>Howellella elegans</i>	
<i>Isorthis orbicularis</i>	
<i>Leptaena rhomboidalis</i>	
<i>Sphaerirhynchia wilsoni</i>	
<i>Strophonella euglypha</i>	
bryozoans	

Less common but important fossils :

<i>Protochonetes ludloviensis</i> (not found below these beds)	} (not found above these beds)
<i>Fardenia pecten</i>	
<i>Shaleria</i> sp. nov.	
<i>Dayia navicula</i>	
<i>Strophonella funiculata</i>	
<i>Cypricardinia</i> spp.	
<i>Liospira striatissima</i>	
<i>Poleumita globosa</i>	
<i>Rhabdocyclus porpitoides</i>	
solitary corals	

These distinctive beds have not previously been separated and appear to have been hitherto included with the Aymestry Limestone because of their faunal affinities.

The standard section for the base of the Lower Bringewood Beds, which is also that for the base of the Bringewoodian Stage, is described in Section VI, p. 141.

SELECTED LOCALITIES

Locality 44 : see Section IV (d) page 133

Locality 19 : see Section IV (b) page 128

Locality 33 : see Section IV (c) page 131

(g) Upper Bringewood Beds

These beds have been called Aymestry Limestone in previous papers. The assumption that the limestone gives rise to the Ludlovian scarp feature is mostly

incorrect in this area ; it does so only in the extreme west and at Mary Knoll. The Upper Bringewood Beds have a maximum thickness of about 150 ft. in the west of the Ludlow district at Downton Gorge, from which they thin eastwards to a minimum of approximately 40 ft. The change from Lower to Upper Bringewood Beds, relatively sharp in the west but more gradual in the east, involves an increased proportion of harder limestone over calcareous siltstone. The typical Upper Bringewood Beds are irregularly bedded, flaggy, silty limestones or irregularly flaggy to nodular, crystalline limestones. Shell bands of *Conchidium knighti* are fairly common, the limestones are sometimes crinoidal, and in places tabulate corals are common. There are thin shaly partings at intervals of several feet.

The fresh limestone is medium grey, weathering to light olive grey ; this latter colour also characterizes the more silty limestone. Some of the more calcareous beds may weather to brown rottenstone. The nodular limestones, with the surrounds to the nodules softened by weathering, assume the "lenticular" texture previously referred to under the Wenlock Limestone.

The fauna of the Upper Bringewood Beds is substantially similar to that of the lower division but strophomenid brachiopods are less abundant, whereas *Conchidium knighti* and compound corals become common.

Common or fairly common fossils :

<i>Conchidium knighti</i>	(found only in these beds)	
<i>Favosites gothlandicus</i>		} (not found above these beds)
<i>Heliolites interstinctus</i>		
<i>Gypidula lata</i>		} (very rare above these beds)
<i>Strophonella euglypha</i>		
solitary corals		
<i>Atrypa reticularis</i>		
<i>Camarotoechia nucula</i>		
<i>Isorthis orbicularis</i>		
<i>Leptaena rhomboidalis</i>		
<i>Sphaerirhynchia wilsoni</i>		
crinoid columnals		

Less common but important fossils :

<i>Brachyprion</i> sp. nov.	} (not found above these beds)
<i>Eospirifer plicatellus</i>	
— <i>radiatus</i>	
<i>Strophonella funiculata</i>	
<i>Dalmanites myops</i>	
<i>Liospira striatissima</i>	
<i>Pleumita globosa</i>	
<i>Rhabdocyclus porpitoides</i>	
stromatoporoids	
<i>Dayia navicula</i>	
<i>Monograptus leintwardinensis</i> var. <i>incipiens</i>	(in higher beds)
<i>Ptilodictya lanceolata</i>	

These beds constitute the familiar Aymestry Limestone of View Edge and Aymestry ; much of the Aymestry Limestone along Corvedale, however, comprises calcareous Lower Leintwardine Beds.

The standard locality for the base of the Upper Bringewood Beds is at Grid Reference 45957352, where the $2\frac{1}{2}$ -Inch (1 : 25000) and 6-Inch O.S. maps show the main source of the stream named Raddle Brook, which flows northwards down the dip slope to join the River Teme about 1,000 yards north-east of Bringewood Forge Bridge. Below this locality the slope of the ground is less than the dip and for about 100 yards the rocky bed of the stream provides a more or less continuous exposure through almost the whole succession of the Upper Bringewood Beds. The base of these hard lime stones causes a distinct change of slope, at which the base of the Upper Bringewood Beds has been taken in the stream profile, and to the south of this (i.e. upstream) is a broader, flat area of the stream bed, about 7 yards in length, on the outcrop of the Lower Bringewood Beds. Above this (at the south side) a low cliff about 4 ft. high exposes the top part of these beds. There is a spring below the cliff, but a lesser stream course descends the higher part of the forested slope and enters the flat area near the spring by a short "waterfall" to the west of the small cliff. Lower Bringewood Beds are also exposed in this "waterfall" and about 10 yards up the stream course above it.

The small cliff exposure shows the typical lithology of the Lower Bringewood Beds, with their thickly flaggy to massive calcareous siltstones and some limestone nodules or lenses. In contrast the Upper Bringewood Beds are hard flaggy lime-stones exposed as a series of bedding planes in the stream.

Both divisions are highly fossiliferous, though the Lower Bringewood Beds are not altogether typical because of an unusual abundance of gastropods and the apparent absence of *Gypidula lata*, *Strophonella euglypha* and *Strophonella funiculata*. The occurrence of *Brachyprion* sp. nov. at this exposure is therefore important. From the basal Upper Bringewood Beds the diagnostic fossils *Conchidium knighti* and *Favosites* were collected. The complete fauna collected from the Lower Bringewood Beds in the small cliff and adjacent "waterfall" is as follows : *Atrypa reticularis*, *Howellella elegans*, *Isorthis orbicularis*, *Sphaerirhynchia wilsoni* and flat gastropods (all common fossils) ; *Chonetes lepisma*, *Leptostrophia filosa* and *Cypri-cardinia subplanulata* (all fairly common) ; *Brachyprion* sp. nov., *Craniops implicata*, *Dayia navicula*, *Leptaena rhomboidalis*, bryozoans, *Cypri-cardinia planulata*, *Pterinea sowerbyi*, " *Murchisonia* " sp., a turreted gastropod, *Cornulites serpularius*, a trilobite hypostoma and fragment, *Hemsiella maccoyana* ?, *Primitia* sp. and a crinoid columnal.

From the basal foot of the Upper Bringewood Beds in the stream bed the following were collected : *Favosites* sp., solitary coral, *Atrypa reticularis*, *Camarotoechia nucula*, *Chonetes lepisma*, *Conchidium knighti*, *Lingula lewisi* (several, in position of growth), *Sphaerirhynchia wilsoni*, *Strophonella euglypha* (very common), a flat gastropod, *Dalmanites myops* and crinoid columnals. Additional fossils collected from higher in the sequence further down the stream are as follows : bryozoa, *Gypidula lata*, *Leptaena rhomboidalis* and " *Murchisonia* " sp.

SELECTED LOCALITIES

Locality 45 : see Section IV (d) page 134

Locality 77 : see Section IV (d) page 138 (Upper Bringewood Beds succeeded sharply by Lower Leintwardine Beds)

Locality 127 : see Appendix 1 page 165 (joint surfaces exposed by landslipping c.f. Locality 22)

Locality 23 : see Section IV (b) page 128

Locality 22 : see Section IV (b) page 128

Locality 20 : see Section IV (b) page 128

Locality 35 : see Section IV (c) page 131

(h) *Lower Leintwardine Beds*

The outcrop of the Lower Leintwardine Beds generally forms the higher part of the dip slope, but at the eastern end of Burrington Hays, as a result of faulting, these beds form the crest of the scarp. The main Ludlovian feature may thus be formed by any one of four stratigraphical divisions, Upper Elton Beds, Lower Bringewood Beds, Upper Bringewood Beds or Lower Leintwardine Beds.

The Lower Leintwardine Beds are approximately 100 ft. thick. In the western part of the district, towards Downton Gorge (e.g. Text-fig. 10, Locality 40) the lithological change from the nodular limestones of the Upper Bringewood Beds is clear and sharp. The Lower Leintwardine Beds here are light olive grey, calcareous, thinly flaggy and shaly, medium-coarse siltstones, with thinly flaggy shelly limestones. Weathering gives a dusty yellowish grey appearance, with the shelly limestones forming dark yellowish-brown rottenstones.

Elsewhere, for example in the standard section for the basal boundary (Locality 30) described on pp. 141-145, the Lower Leintwardine Beds begin with somewhat nodular, irregularly bedded, massive or thickly flaggy limestones. These are followed by better and more thinly-bedded calcareous siltstones, similar to those in the west but richer in calcium carbonate and with a characteristic honeycomb weathering.

In the Lower Leintwardine Beds the characteristic fossils of the Bringewood Beds (see Lawson, 1960 : 117-118) are either absent or very rare, even though the facies contrast is not at all strong near Ludlow itself. Brachiopods remain the dominant fossils.

Common or fairly common fossils :

Monograptus leintwardinensis (not found below these beds)

Sphaerirhynchia wilsoni (not found above these beds)

Chonetes lepisma (not common above these beds)

Atrypa reticularis

Camarotoechia nucula

Dayia navicula

Isorthis orbicularis

Leptaena rhomboidalis

Shaleria ornatella (common in the higher beds)

bryozoans

crinoid columnals (at base)

Less common but important fossils :

<i>Salopina lunata</i>	} (not found below these beds)
<i>Serpulites longissimus</i>	
<i>Beyrichia kloedeni</i> var. <i>torosa</i>	
<i>Protochonetes ludloviensis</i>	
<i>Lingula lata</i>	

proetid trilobite (in highest beds)
Fuchsella amygdalina

There is a distinct change of emphasis in the fauna from east to west, presumably related to the facies change as the muddier and less calcareous basin region is approached. In the west of the area *Dayia navicula*, *Lingula lata* and *Monograptus leintwardinensis* are commoner than in the east but *Atrypa reticularis*, *Camarotoechia nucula*, *Shaleria ornatella* and *Sphaerirhynchia wilsoni* are correspondingly less common. The authors are indebted to Dr. E. V. Tucker for more detailed confirmation of these changes.

These beds are roughly equivalent to the *Dayia* or Mocktree Shales of Elles & Slater (1906).

The standard section for the base of the Lower Leintwardine Beds, which is also that for the base of the Leintwardinian Stage, is described in Section VI on pp. 141-145.

SELECTED LOCALITIES

Locality 77 : see Section IV (d) page 138 (basal Lower Leintwardine Beds of typical western facies following sharply upon limestones of Upper Bringewood Beds)

Locality 129 : see Appendix 1 page 165 (higher part of Lower Leintwardine Beds ; *Monograptus leintwardinensis* common)

Locality 24 : see Section IV (b) page 128 (basal Lower Leintwardine Beds of eastern facies)

Locality 25 : see Section IV (b) page 129 (uppermost Lower Leintwardine Beds)

Locality 261 : see Appendix 1 page 169

(i) *Upper Leintwardine Beds*

In the eastern part of the district, for example in the standard section on the Whitcliffe (see p. 117), the Upper Leintwardine Beds show the same thinly bedded calcareous siltstones, with their characteristic honeycomb weathering, as are found in the bulk of the Lower Leintwardine Beds. Their thickness here reaches a maximum value of 18 ft. Only in the top few feet does the bedding become pronouncedly thicker as in the succeeding Lower Whitcliffe Beds.

In the west, the Upper Leintwardine Beds (only about 5 ft. thick) form lithologically more of a transitional group, resembling the succeeding Lower Whitcliffe Beds rather than the Lower Leintwardine Beds. Here they are irregularly bedded, light olive grey or pale olive, somewhat micaceous and calcareous, flaggy medium siltstones. These weather to pale yellowish brown or yellowish grey. Thin shelly

layers, commonly in a rotten, biscuity condition and dark yellowish brown in colour are characteristic of the western exposures.

The fauna of the Upper Leintwardine Beds combines most of the fauna of the lower division with the increased abundance of the incoming Whitcliffe Bed fossils (Lawson, 1960 : 119). In addition there are several fossils common only in these beds.

Common or fairly common fossils :

<i>Neobeyrichia lauensis</i>	(found only in these beds)
<i>Calymene neointermédia</i>	} (fairly common only in these beds)
<i>Encrinurus</i> sp.	
<i>Atrypa reticularis</i>	} (not found above these beds)
<i>Chonetoida grayi</i>	
<i>Leptaena rhomboidalis</i>	
<i>Shaleria ornatella</i>	
<i>Isorthis orbicularis</i>	(rare above these beds)
<i>Camarotoechia nucula</i>	
<i>Protochonetes ludloviensis</i>	
<i>Dayia navicula</i>	
<i>Salopina lunata</i>	
bryozoans	

Less common but important fossils :

Chonetes lepisma (not found above these beds)
 proetid trilobite
Beyrichia kloedeni var. *torosa*
Monograptus leintwardinensis
Cornulites serpularius

In the west of the area where these beds are less calcareous they are characterized by thin, dark brown, biscuity layers crowded with weathered specimens of *Chonetoida grayi* and *Neobeyrichia lauensis* and often containing *Dayia navicula*, *Calymene neointermédia* and *Encrinurus* sp. Such a development is typical of the *lauensis* Beds of the basin facies. In the east, around Ludlow itself, these bands are less common and the Upper Leintwardine Beds are not so readily distinguished from the Lower Leintwardine Beds. This important division was not recognized by previous authors but appears to have been for the most part included in the *Dayia* or Mocktree Shales of Elles & Slater (1906).

The standard section for the base of the Upper Leintwardine Beds is at Locality 3 on the sketch-map of the Whitcliffe (Text-fig. 7). The map-reference is 50717428 and the line X indicates the position of the section in the sketch of the cliff (Text-fig. 4). In the diagram of the vertical section (Text-fig. 5) A and B comprise hard flaggy calcareous siltstones separated by a thin shale two feet above ground level. The fairly common fossils are *Atrypa reticularis*, *Camarotoechia nucula*, *Dayia navicula*, *Leptaena rhomboidalis*, *Shaleria ornatella* and *Monograptus leintwardinensis*.

"*Dalmanella*" sp., *Lingula lata*, a proetid trilobite and *Goniophora cymbaeformis* have also been found. C is a calcareous siltstone band from one to one and a half inches thick which occurs immediately below a recess formed by the weathering back of a shaly layer. Almost at the base of C there is a thin fossiliferous seam which has yielded *Calymene neointermedia*, *Encrinurus* sp. and *Chonetoides grayi*, a fauna here taken to define the Upper Leintwardine Beds. Of other fossils, *Shaleria*

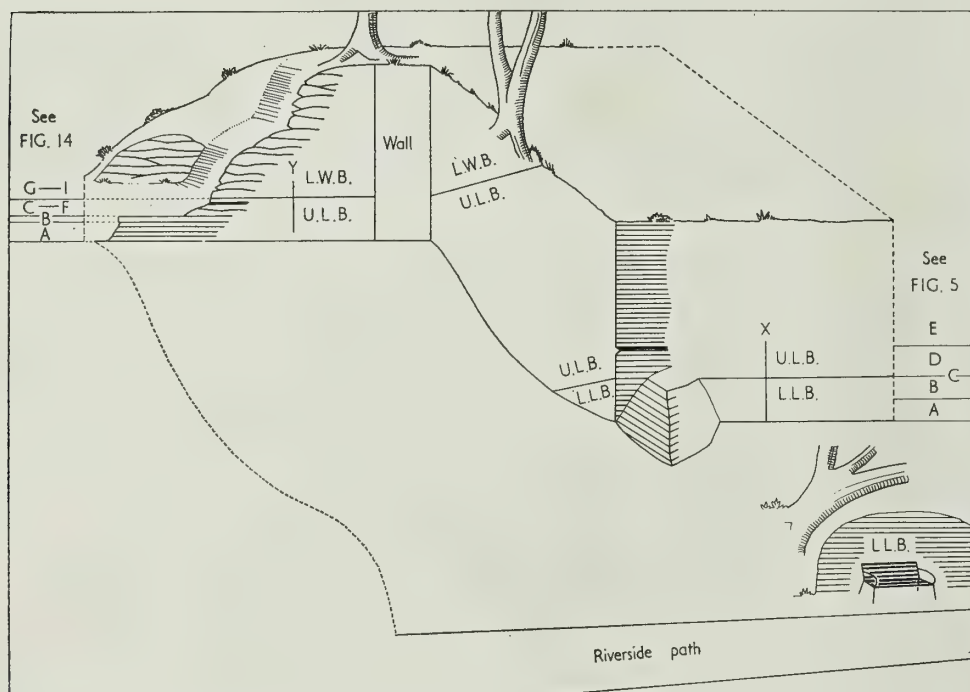


FIG. 4. Sketch of part of the Whitcliffe showing the positions of the standard sections for the boundary between the Lower Leintwardine Beds and the Upper Leintwardine Beds (marked X), and the boundary between the Upper Leintwardine Beds and the Lower Whitcliffe Beds (marked Y). For explanation and reference to other illustrations see pp. 117 and 145.

ornatella is common and *Atrypa reticularis*, *Chonetes lepisma*, *Camarotoechia nucula*, "*Dalmanella*" sp., *Dayia navicula*, *Leptaena rhomboidalis*, *Lingula lata*, a proetid, *Fuchsella amygdalina*, and *Monograptus leintwardinensis* also occur. Some phosphatized fragments have been noted. The base of the Upper Leintwardine Beds is defined by the bottom of this bed C. It is succeeded by flaggy calcareous siltstones, some of which display small-scale current bedding. The highest beds of D are more shaly and form a recess which is particularly marked in the middle section of the cliff face which runs at right angles to the river.

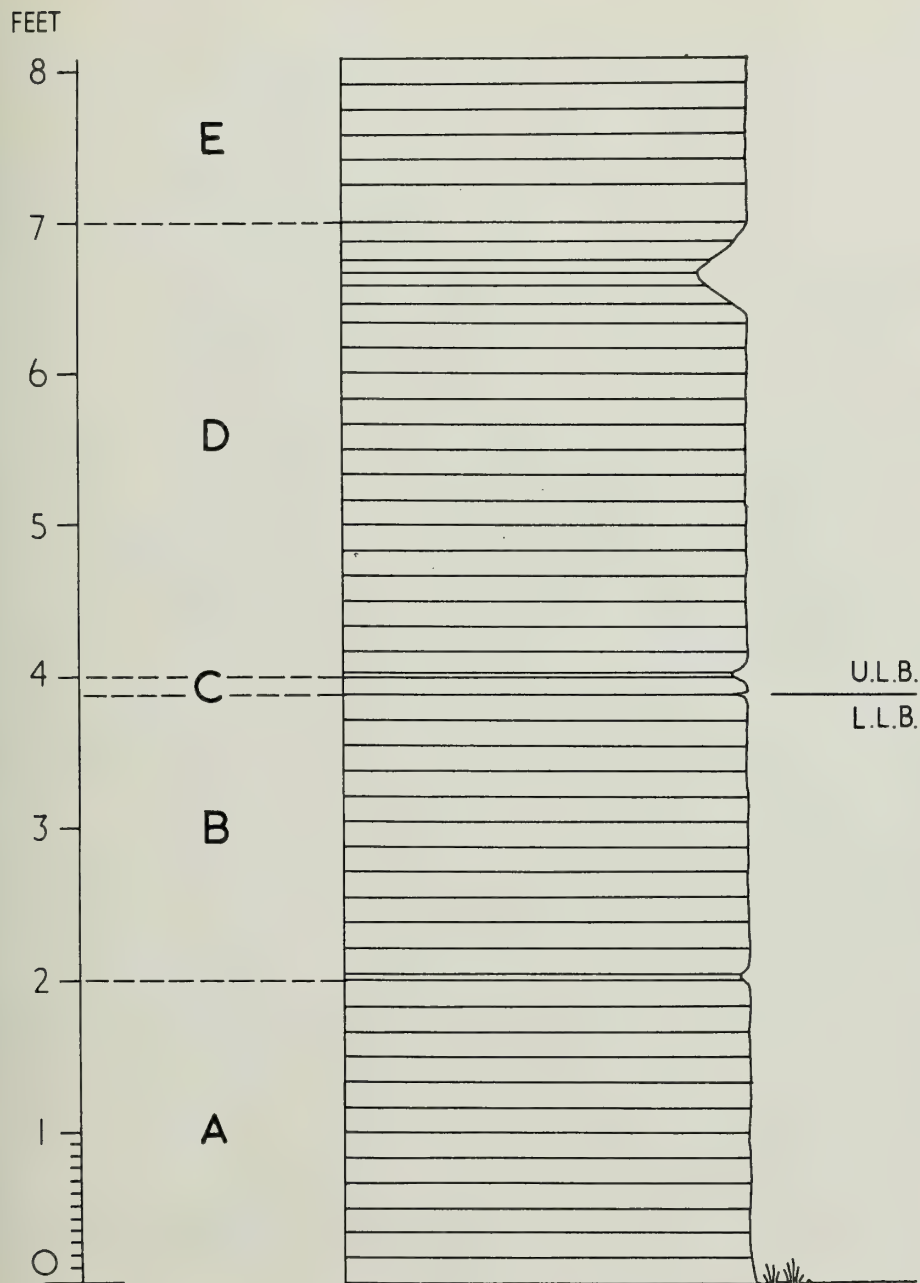


FIG. 5. Diagrammatic section showing the position of the boundary between the Lower Leintwardine Beds and the Upper Leintwardine Beds on the Whitcliffe (for explanation see p. 117).

SELECTED LOCALITIES

- Locality 121 : see Appendix 1 page 165 (Upper Leintwardine Beds of western facies with bands of *Chonetoides grayi* and *Neobeyrichia lauensis*)
- Locality 125 : see Appendix 1 page 165 (western facies)
- Locality 129 : see Appendix 1 page 165 (discontinuous trackside exposure with Lower Leintwardine Beds to south and Lower Whitcliffe Beds to north ; western facies of Upper Leintwardine Beds)
- Locality 26 : see Section IV (b) page 129 (facies of intermediate character with *Shaleria ornatella*, trilobites and *Neobeyrichia lauensis*)
- Locality 27 : see Section IV (b) page 129 (as above)
- Locality 11 : see Section IV (a) page 126 (eastern facies without *Neobeyrichia lauensis*)

(j) *Lower Whitcliffe Beds*

Extensive outcrops of Whitcliffe Beds form the lower dip slopes round the plunging Ludlow Anticline. The Lower Whitcliffe Beds, approximately 80 ft. thick, are irregularly bedded, massive or thickly flaggy, more or less micaceous, somewhat calcareous, coarse to medium siltstones, with a large scale conchoidal or crudely blocky fracture. In colour they vary from medium grey in the fresh, more calcareous beds to shades of greenish grey and light olive grey. Weathering eventually produces a dusky yellow appearance. There are some shaly partings and some smoothly bedded, thinly flaggy siltstones. Calcareous nodules are present and may reach about 12 in. in size. The massive appearance of the beds is noticeable in the steeper part of Downton Gorge, in parts of the Whitcliffe and in various old quarries throughout the district. In smaller exposures the relatively thick bedding and the crude irregularity of both bedding and fracture are often conspicuous.

The base of the Lower Whitcliffe Beds cannot be precisely recognized lithologically as some of the characteristic features are developed in part at least of the Upper Leintwardine Beds. Slump bedding is rare within the group, but the top is marked by the "Concretion-Band" of Elles & Slater (1906), a slump band about 9 to 18 in. in thickness which is exposed at various points within the district (e.g. Whitcliffe, Clive Cottages Quarry, Downton Gorge). The band shows considerable variation in both the intensity and character of the slumping and in some cases (e.g. Downton Gorge and see also Whitaker, 1962) there are several such bands close together. That the band is not in fact "concretionary" is shown by the bending over of shell bands in response to the slump folds.

Most of the elements of the Leintwardine Bed fauna (Lawson, 1960 : 119) disappear at the base of the Lower Whitcliffe Beds but rare survivors may be found. In the Whitcliffe Beds as a whole, brachiopod species, particularly articulate forms, are few ; mollusca become relatively more important, annelids are fairly common, but no graptolites have been found. In the Lower Whitcliffe Beds fossils are not abundant.

Common or fairly common fossils :

Dayia navicula (in lower beds only : not found above)

Camarotoechia nucula
Protochonetes ludloviensis (often of small size)
Salopina lunata
Fuchsella amygdalina
Michelinoceras imbricatum
Serpulites longissimus

Less common but important fossils :

Homalonotus knighti
Beyrichia kloedeni var. *torosa*
Nuculites spp.
Michelinoceras bullatum

These beds are the Lower Whitcliffe or *Rhynchonella* Flags of Elles & Slater (1906).

The standard section for the base of the Lower Whitcliffe Beds, which is also that for the base of the Whitcliffian Stage, is described in Section VI on pp. 145-146.

SELECTED LOCALITIES

Locality 49 : see Section IV (d) page 134

Locality 50 : see Section IV (d) page 134

Locality 53 : see Section IV(d) page 134 (Lower Whitcliffe Beds succeeded by Upper Whitcliffe Beds ; good exposure of slump structures at top of lower division)

Locality 28 : see Section IV (b) page 129

Locality 8 : see Section IV (a) page 126

Locality 29 : see Section IV (c) page 129 (*Dayia navicula* fairly common)

(k) *Upper Whitcliffe Beds*

The Upper Whitcliffe Beds are approximately 100 ft. thick. The slump band which is taken as the top of the Lower Whitcliffe Beds coincides approximately with a change in lithology from the thicker and more irregular bedding seen below. In the absence of the marker band it would be difficult to select a precise lithological boundary within the transitional strata. The typical Upper Whitcliffe Beds are well bedded, pale olive to light olive grey, more or less micaceous, clean, well sorted, medium to coarse siltstones. There are more prominent, compact, flaggy calcareous beds within the slightly more irregular flaggy and shaly siltstones. There is often a laminated appearance, related to a smaller scale development of more calcareous layers. Shelly limestones are commonly present. Weathering produces a characteristic dusky yellow colour, with the more calcareous beds and laminae, together with the shelly limestones, often reduced to dark yellowish brown rottenstones. Small-scale false bedding is frequently developed and there are occasional slump bands, notably an apparently impersistent thin bed about 11 ft. from the base.

Fossils are commoner in the Upper Whitcliffe Beds than in the lower division, brachiopods, *Salopina lunata* in particular, being more abundant.

Common or fairly common fossils :

Camarotoechia nucula

Beyrichia kloedeni var. *torosa*

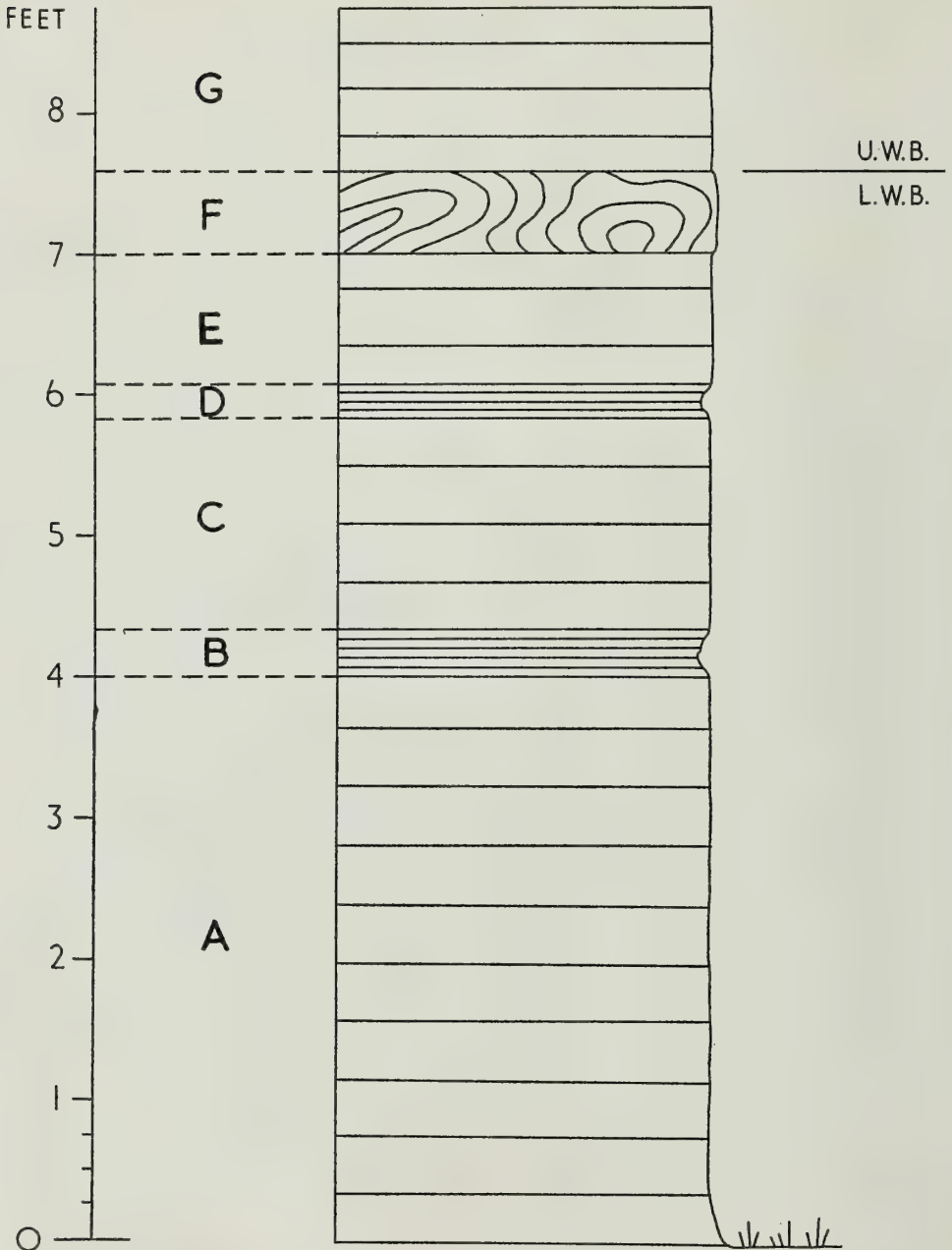


FIG. 6. Diagrammatic section showing the position of the boundary between the Lower Whitcliffe Beds and the Upper Whitcliffe Beds in the Whitcliffe Quarry (for explanation see p. 123).

Protochonetes ludloviensis
Howellella elegans (in highest beds)
Salopina lunata

Fuchsella amygdalina
Pteronitella retroflexa
Serpulites longissimus

Less common but important fossils :

Craniops implicata
Orbiculoidea rugata
Acastella cf. *spinosa*
Nuculites spp.

Loxonema sp.
Michelinoceras bullatum
 — *imbricatum*
Cornulites serpularius

These beds constitute the Upper Whitcliffe or *Chonetes* Flags of Elles & Slater (1906).

The standard locality for the base of the Upper Whitcliffe Beds is the well known old quarry face (50947414) on the Whitcliffe, about 350 yards west-south-west of Ludford Bridge. The quarry is shown as Locality 6 on the sketch-map (Text-fig. 7), and a diagrammatic vertical section of the lower part of the face is given in Text-fig. 6.

Although typical Lower and Upper Whitcliffe Beds can be readily distinguished lithologically (pp. 120, 121), rock types characteristic of each division may occur in the other, making identification in small exposures uncertain. There is also a stratigraphical transition between the two divisions. The faunal differences between them (pp. 120, 123) are slight and depend upon the abundance of certain forms in the Upper Whitcliffe Beds rather than upon the presence of any diagnostic species. Accordingly an arbitrary line must be taken as the base of the Upper Whitcliffe Beds and it is appropriate that this should coincide with that chosen by Elles & Slater (1906) for the boundary between their *Rhynchonella* Flags and *Chonetes* Flags. The base has therefore been taken at the base of the bed above a persistent slump band (the "Concretion-Band" of Elles & Slater), which, as mentioned on page 120, can be seen at several localities in the district.

As shown in the section (Text-fig. 6) the base of the Upper Whitcliffe Beds is about 7 ft. 6 in. above the bottom of the quarry face. The slump band (F) is here about 7 in. thick. The calcareous siltstones below it are interrupted by two prominent shaly bands, whose positions are shown on the diagram. The upper one (D) is 2 to 3 in. thick and the lower (B) 2 to 6 in.

Another slump band is present in this quarry about 11 ft. above the base of the Upper Whitcliffe Beds. This is seen also in Clive Cottages Quarry (see p. 126), though it is less persistent there than the lower band. At the standard locality the upper slump band is set within strata which show the lithology of the Upper Whitcliffe Beds. If a line were to be attempted here between the two lithological types it would approximate to the position of the lower slump band.

SELECTED LOCALITIES

Locality 52 : see Section IV (d) page 134

Locality 54 : see Section IV (d) page 134

Locality 56 : see Section IV (d) page 135 (uppermost Upper Whitcliffe Beds with *Howellella elegans* common and a thin band crowded with *Craniops implicata*)

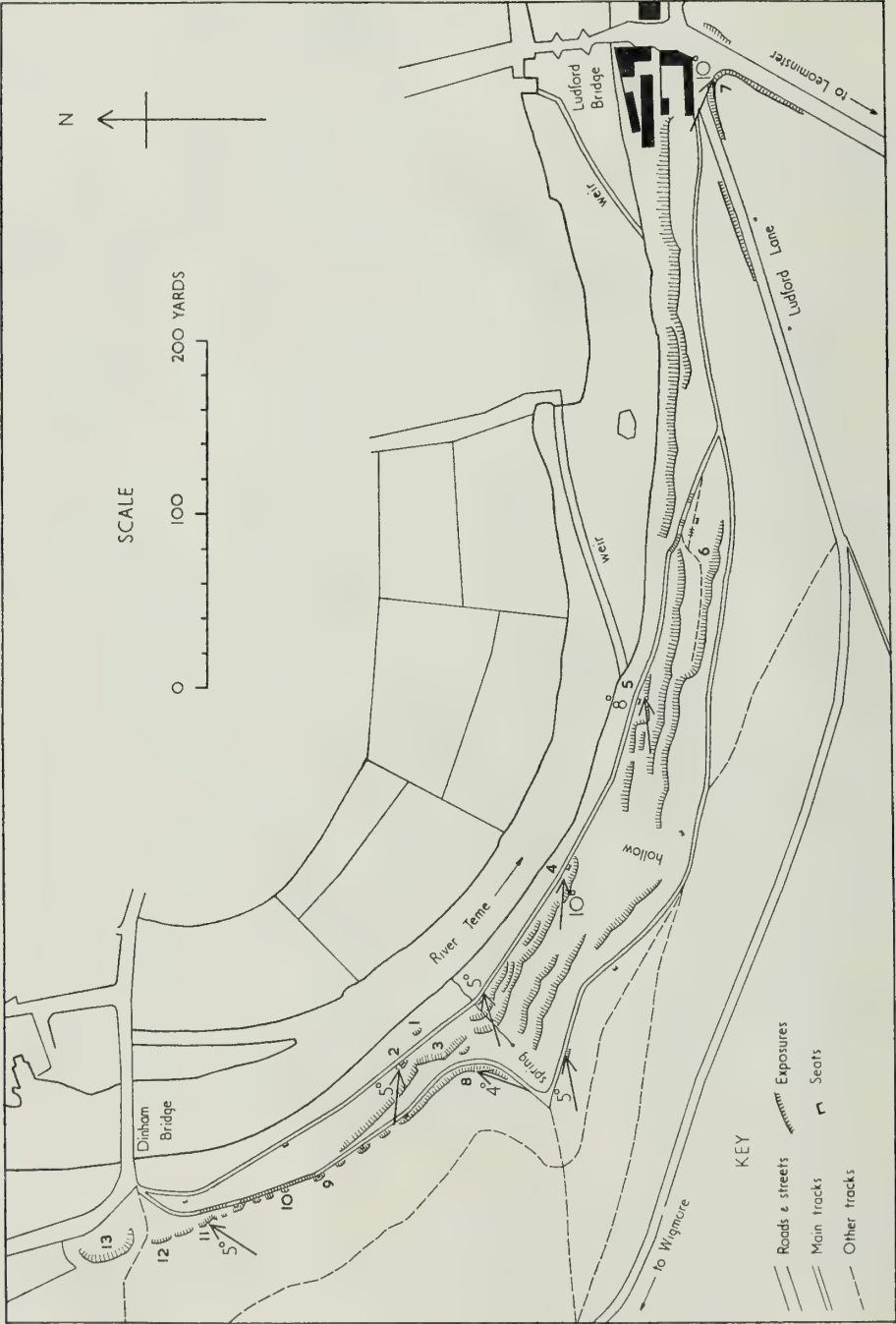


FIG. 7. Sketch-map of the Whitcliffe showing localities described in Section IV (a), pp. 125-126.

Locality 214 : see Appendix 1 page 168

Locality 255 : see Appendix 1 page 169

Locality 220 : see Appendix 1 page 168

(1) *Ludlow Bone Bed*

The Downtonian rocks of the Ludlow district were described in detail by Elles & Slater (1906). No additional description of their lithology and fauna is given here, though sections in these rocks are referred to in the accounts of the Whitcliffe (p. 126) and Downton Gorge (p. 135).

Following White (1950), the present writers have taken the base of the Ludlow Bone Bed as marking the base of the Downtonian Stage and hence of the Lower Old Red Sandstone Series. For the full and precise delimitation of the Whitcliffian Stage (and the Upper Whitcliffe Beds) a standard section for the base of the Downtonian is required. The opportunity is taken to define this standard section and a description of the locality is given in Section VI, p. 146.

Other localities at which the Ludlow Bone Bed (i.e. the base of the Downtonian) may be seen are as follows :

Locality 57 : see Section IV (d) page 135

Locality 137 : see Appendix 1 page 165 (uppermost Whitcliffe Beds, Ludlow Bone Bed, and, 2 ft. 6 in. higher, Downton Bone Bed with associated *Platyschisma helicites* (J. de C. Sowerby))

IV. DETAILED DESCRIPTIONS OF IMPORTANT AREAS AND SECTIONS

(a) *Whitcliffe*

The principal exposures on the Whitcliffe are shown in Text-fig. 7. The geological lines have been omitted to avoid confusion.

Along the riverside path southwards from Dinham Bridge, the main axis of the Ludlow Anticline is crossed before the first exposures occur. At locality (1) (50747428) there is a small outcrop of Lower Leintwardine Beds, the lowest stratigraphical division represented on the Whitcliffe although Elles & Slater (1906 : 202) mapped these strata as Aymestry Limestone, with *Conchidium knighti* and *Strophonella euglypha*. Behind the seat at (2) (50717429) the Lower Leintwardine Beds contain *Atrypa reticularis*, *Camarotoechia nucula*, *Dayia navicula*, *Isorthis orbicularis*, *Leptaena rhomboidalis*, *Shaleria ornatella* and *Monograptus leintwardinensis* (all fairly common). On the main cliff at (3) the Upper Leintwardine Beds are fully exposed and these standard sections for the base of this division and for the base of the Whitcliffian stage are fully described on pp. 117, 145. Bands with *Chonetoides grayi*, *Calymene neointermedia* and *Encrinurus* sp. occur ; the rest of the fauna is similar to that of the Lower Leintwardine Beds except that *Chonetes lepisma* is less common and *Protochonetes ludloviensis* and *Salopina lunata* are more common. These beds descend to the track beyond the spring and are last exposed in this riverside section at locality (4) (50827421). At (5) (50907417) the more thickly and irregularly bedded Lower Whitcliffe Beds occur, with *Camarotoechia nucula*, *Protochonetes ludloviensis*, *Salopina lunata*, *Fuchsella amygdalina*, *Michelinoceras imbricatum* and *Serpulites longissimus* as the commonest fossils. The rock steps are formed by massive beds

of the same division and in the Whitcliffe Quarry behind locality (6) (50967414) the base of the Upper Whitcliffe Beds has been defined at the top of a conspicuous and persistent slump band (see p. 123 and Text-fig. 6). The Upper Whitcliffe Beds are more fossiliferous than the lower division, and *Protochonetes ludloviensis* and *Salopina lunata* are relatively more common. This applies particularly to the uppermost beds which can be examined at the junction of "Ludford Lane" (i.e. the Whitcliffe road leading to Wigmore), and the road to Leominster (locality (7) (51237413)). This is the well-known outcrop of the Ludlow Bone Bed and the sequence here is referred to on p. 146.

Returning to Dinham Bridge by the track along the top of the Whitcliffe the first important exposure is at (8) (50717425) where Lower Whitcliffe Beds are seen. They are not very fossiliferous but *Camarotoechia nucula*, *Protochonetes ludloviensis* and *Salopina lunata* can easily be found. Further down the path and near the base of this same division a specimen of *Calymene* has been found, associated with *Camarotoechia nucula*, *Protochonetes ludloviensis*, *Fuchsella amygdalina*, *Bucanopsis expansus* and *Serpulites longissimus*. Lower Whitcliffe Beds still occur at (9) but the next small outcrop down the path (locality (10)) is of Upper Leintwardine Beds with *Shaleria ornatella* common. The change in lithology from the thickly and irregularly bedded Lower Whitcliffe Beds to the honeycombed, more thinly bedded Upper Leintwardine Beds is striking. At (11) (50627440) the lowest beds of the exposure are Lower Leintwardine Beds with *Dayia navicula* and *Chonetes lepisma* more frequent, but 5 ft. above the base *Calymene neointermedia*, *Encrinurus* sp. and *Chonetoides grayi* appear, indicating the Upper Leintwardine Beds. The authors have, however, failed to find an undoubted specimen of *Neobeyrichia lauensis*, the truly diagnostic fossil for this division, anywhere on the Whitcliffe. A small fault separates this exposure from locality (12) which is of downthrown Lower Whitcliffe Beds. These also occur in the small quarry at (13) (50627445) but are best studied at Clive Cottages Quarry (50517458) which is just off the sketch map to the north. In this large quarry the slump band at the top of the Lower Whitcliffe Beds is displayed, succeeded by a considerable thickness of Upper Whitcliffe Beds, including some less persistent slump structures.

Elles & Slater (1906: 202) appear to have mapped the honeycombed and calcareous Leintwardine Beds as the Aymestry Limestone, in spite of the frequent occurrence of *Dayia navicula* and the absence of corals, *Strophonella funiculata* and (although not according to Elles & Slater) *Conchidium knighti* and *Strophonella euglypha*. The basal Lower Whitcliffe Beds contain *Dayia navicula* and these strata seem to have been misidentified as the Mocktree Shales, but they lack all the other characteristic elements of the *Dayia navicula* fauna (e.g. *Atrypa reticularis*, *Chonetes lepisma*, *Isorthis orbicularis*, *Leptaena rhomboidalis*, *Shaleria ornatella*, *Sphaerirhynchia wilsoni* and *Monograptus leintwardinensis*).

(b) Wigmore Road

This section (see Text-fig. 8) permits the ascending sequence from Wenlock Limestone to the Whitcliffe Beds to be studied along an easily accessible route.

From a viewpoint on the road (456714) just over a mile to the south-west of

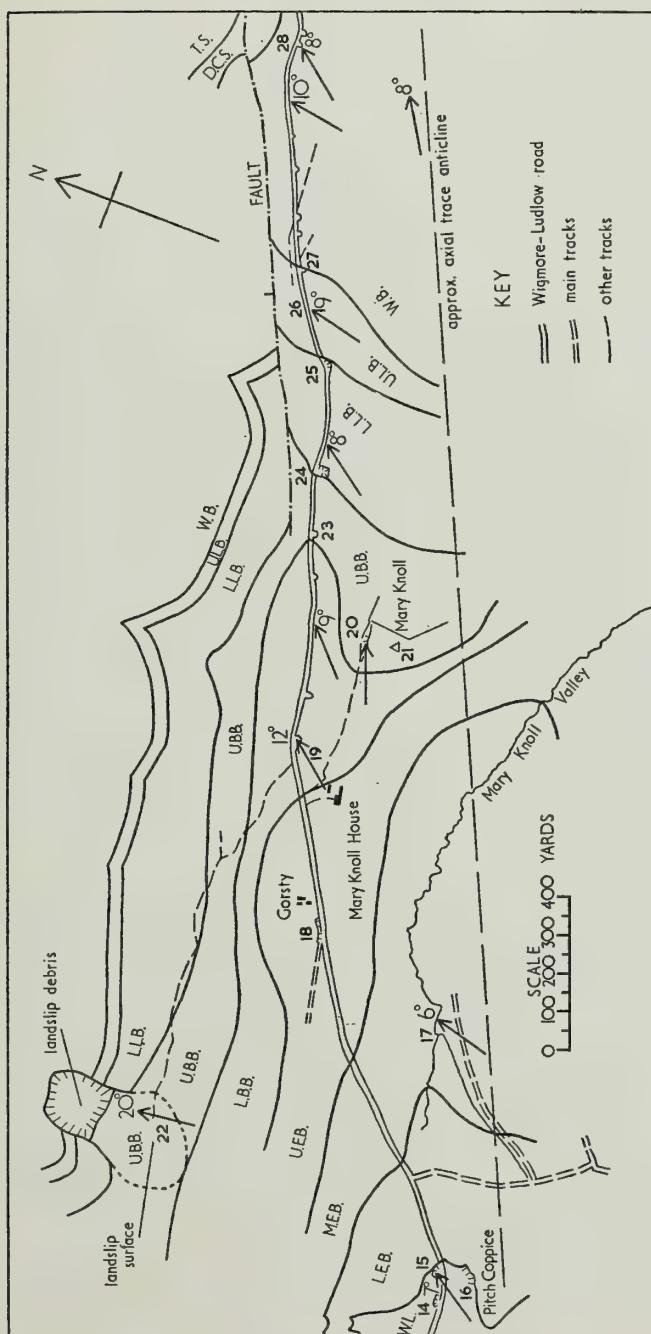


FIG. 8. Sketch-map showing localities near the Wigmore road as described in Section V (b), pp. 126-130.

Pitch Coppice, the topographic expression of the successive beds can be clearly seen. The route from this point via Pitch Coppice, along the Wigmore Road to Whitcliffe, provides a traverse almost along the anticlinal axis.

Wenlock Shales can be seen in the stream along the south side of the road, for example at (46257220), and the succeeding Wenlock Limestone is exposed in two roadside quarries at locality (14) (47167301) and locality (15) (47227304) where the change from the lower flaggy limestone to the upper nodular limestone can be noted. Fossils are scarce, but include *Atrypa reticularis*, *Rhipidomella hybrida*, *Eospirifer radiatus* and *Sowerbyella* sp., as well as reddened tubular bryozoa.

In the wood immediately opposite locality (15) is a third Wenlock Limestone exposure, locality (16) (47267301), which shows the junction with the overlying Lower Elton Beds. This is a standard locality and is described in detail on pp. 139-141. Locality (17) comprises a number of small exposures in the stream (47777324) at which fossiliferous Middle Elton Beds can be examined. *Chonetoides grayi*, *Dalmanites myops* and small orthoconic nautiloids are present, but graptolites of the *Monograptus nilssoni*-*M. scanicus* assemblage are difficult to find.

Upper Elton Beds are well exposed at the entrance to Gorsty Farm, locality (18) (47897357) and along the adjacent level Forestry Commission track. Good specimens of *Monograptus tumescens* are common here. *Brachyprion* sp. nov., *Slava interrupta* and *Lingula* sp. may also be seen. Further along the road is locality (19) (48287377), a small overgrown quarry on the south side of the road which exposes the more calcareous Lower Bringewood Beds. Fossils are not very abundant, but brachiopods rather than graptolites are likely to be found. In particular, *Brachyprion* sp. nov., which is common, *Shaleria* sp. nov., *Gypidula lata*, *Leptaena rhomboidalis*, *Strophonella filosa*, *Chonetes lepisma* and *Lingula lewisi*. From a field gate immediately east of Mary Knoll House, a track leads to locality (20) (48557369), a disused quarry at the north end of Mary Knoll, which exposes about 12 ft. of Upper Bringewood Beds yielding their characteristic fauna including *Conchidium knighti*, *Leptaena rhomboidalis*, *Atrypa reticularis*, *Strophonella euglypha*, *Gypidula lata*, *Favosites* and *Poleumita globosa*.

The Forestry Commission track which starts immediately opposite locality (19) leads westwards to the large landslip scar, locality (22) (47337382), which provides an excellent and extensive exposure of one bedding plane in the Upper Bringewood Beds. The orientation and distribution of characteristic fossils such as *Strophonella euglypha*, *Atrypa reticularis*, *Gypidula lata*, *Isorthis orbicularis* and *Favosites* can be studied on this surface. The landslip, which occurred in 1947, involved about 11 ft. of flaggy limestones and flaggy calcareous siltstones which moved on a thin seam of shale, no doubt as a result of the near coincidence of dip and ground slope.

Further down the Wigmore Road from locality (19), a series of roadside exposures occurs on the south side. At the first of note, locality (23) (48747389), fossiliferous Upper Bringewood Beds yielding *Conchidium knighti* and associated fauna can be seen again. Slightly higher beds in the largest quarry, locality (24) (48887392), have previously been regarded as Aymestry Limestone, but their fauna is undoubtedly that of the Lower Leintwardine Beds and the misidentification serves to emphasize how in this eastern part of the area the middle Ludlovian calcareous

phase persists into the Leintwardine Beds. Some 30 ft. of beds are exposed in this quarry. The lowest 4 ft. are tough, blue grey limestone and calcareous siltstone with a prominent band of *Atrypa reticularis* at the top. The succeeding 10 ft. of massive calcareous siltstone with nodules of limestone weathers to a honeycomb surface and yields *Isorthis orbicularis*, *Atrypa reticularis* and *Chonetes lepisma*. Higher strata are poorly bedded and lack nodules. *Isorthis orbicularis* becomes more common and in the highest beds, which can also be seen on the roadside to the north-east, this brachiopod is very common and associated with *Chonetes lepisma*, *Sphaerirhynchia wilsoni*, *Leptostrophia filosa* and rare crinoid columnals. Although *Dayia navicula* is not seen, the apparent absence of *Leptaena rhomboidalis*, *Conchidium knighti*, *Gypidula*, *Strophonella euglypha* and corals, indicate an age younger than that of the Upper Bringewood Beds. In the immediately succeeding beds, exposed on the roadside, *Dayia navicula* and *Fuchsella amygdalina* are found with *Isorthis orbicularis*, *Chonetes lepisma*, *Camarotoechia nucula* and *Sphaerirhynchia wilsoni*—a typical Lower Leintwardine Beds fauna. The calcareous facies here is emphasized by the rare occurrence (exceptional at this horizon) of corals.

Locality (25) (49107399) is a roadside quarry which descends below road level and reveals the higher part of the Lower Leintwardine Beds. The lowest 3 ft. of beds exposed have yielded *Monograptus leintwardinensis*, *Dayia navicula*, *Strophonella euglypha*, *Camarotoechia nucula*, *Shaleria ornatella* and *Leptaena rhomboidalis*, which are all common. In the succeeding 4 ft. of beds, *Fuchsella amygdalina* (in bands) and *Shaleria ornatella* are common, associated with *Atrypa reticularis*, *Isorthis orbicularis*, *Chonetes lepisma*, *Leptaena rhomboidalis*, and *Dayia navicula*. The higher and less accessible beds have yielded mainly *Shaleria ornatella* and *Dayia navicula* which are common, *Isorthis orbicularis*, and *Pteronitella retroflexa*. Above road level, the highest Lower Leintwardine Beds contain *Isorthis orbicularis*, *Shaleria ornatella*, *Chonetes lepisma*, *Leptaena rhomboidalis*, *Fuchsella amygdalina*, *Dayia navicula*, and *Craniops implicata*.

Upper Leintwardine Beds make the ground immediately above the quarry and can be examined in two small exposures down the road, locality (26) (49227407) and locality (27) (49307412) both of which yield the typical fauna, although not readily. At locality (26), some 8 ft. of beds are exposed. *Neobeyrichia lauensis*, *Shaleria ornatella*, *Salopina lunata*, *Isorthis orbicularis*, *Camarotoechia nucula*, *Protochonetes ludloviensis* and bryozoans are the commonest fossils together with *Atrypa reticularis*, *Encrinurus* sp., *Calymene neointermedia*, *Orbiculoidea rugata* and *Serpulites longissimus*.

Locality (27) has also yielded most of these species, especially *Neobeyrichia lauensis*, *Shaleria ornatella* and *Calymene neointermedia*.

At locality (28) (49797430) Lower Whitcliffe Beds are well exposed. The poorly bedded rubbly siltstone includes concretions up to 12 in. long. Fossils are sporadic, but *Protochonetes ludloviensis* and *Camarotoechia nucula* are common, sometimes found covering bedding planes. *Salopina lunata*, *Michelinoceras bullatum*, *Goniorhynchus cymbaeformis*, *Kionoceras angulatum*, *Fuchsella amygdalina* and *Serpulites longissimus* have also been found here.

From this point the road crosses unexposed Whitcliffe Beds to its junction with

the main Ludlow to Leominster road, where the highest Whitcliffe Beds, Ludlow Bone Bed and Downton Castle Sandstone can be examined on the south side of the corner (see p. 146).

(c) *Mary Knoll Valley*

The lower part of the Mary Knoll valley, around Sunnyhill Cottages, displays good exposures of the Ludlovian succession from the Lower Bringewood Beds to the Lower Whitcliffe Beds inclusive. There is a Forestry Commission road up the

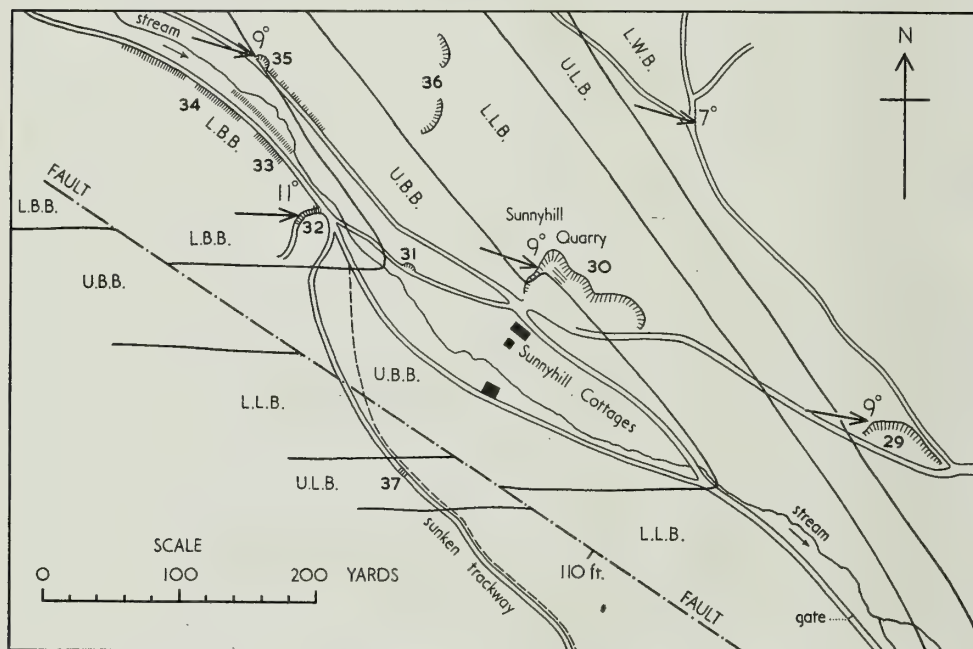


FIG. 9. Sketch-map showing localities in the Mary Knoll Valley as described in Section V (c), pp. 130-131.

western flank of the valley, from the old Leominster road at Overton to the Wigmore road near Pitch Coppice. Text-fig. 9 shows the principal exposures in the Sunnyhill area. In the quarry at locality (29) (49737244) the Lower Whitcliffe Beds are of particular interest because of the common occurrence of *Dayia navicula*; *Protochonetes ludloviensis* is also fairly common and *Camarotoechia nucula* abundant. *Salopina lunata*, *Schizocrania striata*, *Serpulites longissimus*, *Michelinoceras* sp., and *Fuchsella amygdalina* also occur. These strata are again exposed alongside the track above the quarry. Descending the road to the main Sunnyhill Quarry (locality 30) (49537255) the standard section for the base of the Leintwardinian stage can be examined (see pp. 141-145 for details). In the small quarry at locality (31) (49437255) the lowest Upper Bringewood Beds occur, being more thinly bedded and less calcareous than the higher strata of this division. A descending sequence

in Lower Bringewood Beds can be studied at localities (32), (33) and (34). At (32) (49367260) the following fossils were collected : *Atrypa reticularis*, *Howellella elegans*, *Strophonella euglypha*, *Strophonella funiculata* and crinoid columnals. In the road-side bank at (33) a large fauna was found : *Gypidula lata* (fairly common), *Atrypa reticularis*, *Brachyprion* sp. nov., *Chonetoidea grayi*, *Fardenia pecten*, *Howellella elegans*, *Leptaena rhomboidalis*, *Leptostrophia filosa*, *Shaleria* sp. nov., *Sphaerirhynchia wilsoni*, *Strophonella euglypha*, *Dalmanites myops*, *Encrinurus* sp., *Beyrichia* sp., solitary corals and *Cornulites serpularius*. At locality (34), the beds are softer and fossils less common ; *Leptaena rhomboidalis* and bryozoans were collected. About 500 yards north-westwards along the road from locality (34) the track which rises to the left leads to the standard section for the base of the Bringewoodian stage, fully described on p. 141. Opposite the commencement of this track there is a bridge over the Mary Knoll stream, and a return can be made along the road on the eastern side. There are several exposures of Upper Elton Beds in the stream (e.g. at 48927287). At locality (35) (49337268) in Text-fig. 9 there is a small quarry in the basal Upper Bringewood Beds, which are flaggy like the Lower Bringewood Beds but harder and more calcareous. Some solitary corals occur : *Atrypa reticularis* and *Strophonella euglypha* are fairly common and *Brachyprion* sp. nov., *Eospirifer radiatus*, *Howellella elegans*, *Leptaena rhomboidalis*, *Shaleria* sp. nov and *Strophonella funiculata* also occur. Further exposures follow in the bank of the road and the fossils include *Favosites*. *Conchidium knighti* has been found only in the Upper Bringewood Beds of the main Sunnyhill Quarry (locality (30)) in this area and even there it is not common. In the flanks of a broad gully above the road there are crags (36) in Lower Leintwardine Beds with Upper Leintwardine Beds at the very top. Bringewood Beds and Lower Leintwardine Beds can also be seen in the stream when the water is low.

The Sunnyhill Fault has been mapped mainly on the evidence from small exposures and debris in tree roots along the overgrown trackway ; there seems little doubt that the Upper Leintwardine Beds have been downthrown at least 100 ft. on the west side of the fault. At locality (37) (49427242) they yielded *Camarotoechia nucula*, *Chonetoidea grayi*, *Protochonetes ludloviensis*, *Calymene neointermedia* and *Serpulites longissimus*.

(d) Downton Gorge and Burrington

The gorge of the River Teme between Burrington and Downton Castle, cut by the overflow waters of the glacial lake of the Vale of Wigmore (see Dwerryhouse & Miller, 1930 : 116, 117), provides the western boundary of the district described in this paper. The area to the west of the river has been described recently by Whitaker (1962) and the following paragraphs refer to a sequence of exposures along and near its eastern bank. These exposures range from Wenlock Shales to Downtonian and most of the stratigraphical divisions are well displayed.

The area around Burrington village has long been well known for its Wenlock Shale fossils. Exposures in the sunken lanes and old quarries to the south of the village are now overgrown, but the best exposures in the Ludlow district of Wen-

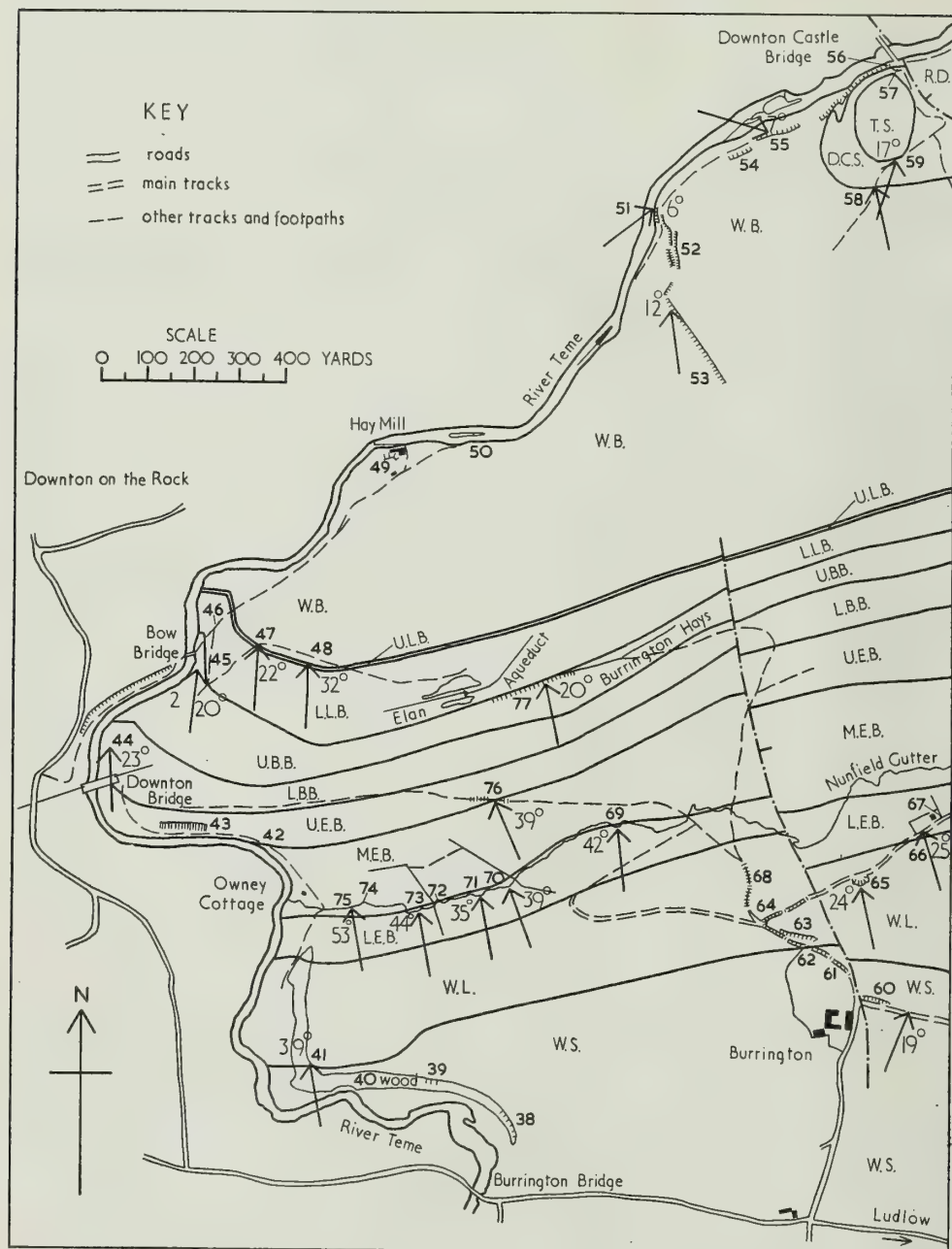


FIG. 10. Sketch-map showing localities in the Downton Gorge and Burrington area as described in Section IV (d), pp. 133-138.

lockian and lowest Ludlovian strata are still to be seen to the north and north-west of Burrington.

(1) *Downton Gorge* (see Text-fig. 10)

The eastern bank of the Teme may be reached by a field gate on the north side of the road a short distance to the east of Burrington Bridge (43607207). The steep, wooded slope of the old river cliff, rising from the alluvial flat, shows a number of small exposures of Wenlock Shales of which localities (38) and (39) are examples. The typical, light coloured, dusty weathering is seen and the fauna is an ill-preserved one of small brachiopods, orthoconic nautiloids, and the ostracod *Hemsiella maccoyana*. At locality (40) (43347227) where a track, beyond a gate, runs between river and wooded slope the bank has been cut back into Wenlock Shales. In this fresher exposure a more thickly bedded appearance and a large-scale conchoidal fracture are noticeable. *Gothograptus nassa* and *Monograptus dubius* were collected here, together with *Cyrtia exporrecta*. Flaggy limestones of the lowest Wenlock Limestone form a capping to the steep slope and are very poorly exposed at locality (41) (43277232).

Nunfield Gutter, the stream joining the Teme from the east near Owney Cottage, provides excellent exposures in the upper part of the Lower Elton Beds and the basal Middle Elton Beds, which are described later under (2).

Beyond Owney Cottage a path leads north-westwards along the river bank below an impressive wooded feature made by the Middle Elton Beds. At locality (42) (43237273) the first few small exposures just above the path are of uppermost Middle Elton Beds. These are relatively soft, shaly and thinly flaggy siltstones with graptolites (*Monograptus comis* and *M. dubius* collected), orthoconic nautiloids and common fragments of *Lingula lata*. Most of the exposures in the steep slope above the river, for example the large crags at (43) (43037280), are of typical Upper Elton Beds with their hard, smoothly bedded, flaggy siltstones. False-bedding, slump-structures, and especially crinkle markings, are all to be seen. *Monograptus tumescens* is very common but there are few other fossils.

At the top of the slope, immediately below the footpath, there are a few exposures of basal Lower Bringewood Beds. Bands of shelly fossils appear and the following were collected: *Chonetes minimus*, *Protochonetes ludloviensis*, *Howellella elegans*, *Shaleria* sp. nov., *Strophonella funiculata* and *Dalmanites myops*.

North of the Birmingham Corporation Elan Aqueduct at Downton Bridge there is no clear riverside path, but two small old quarries (locality (44)), one at, and one a little to the north of, the dip arrow (42897296) are easily located in a bank under trees. The typical flaggy calcareous siltstones of the Lower Bringewood Beds, with their limestone bands and lenticles, are here very fossiliferous. The fauna includes: *Chonetes minimus*, *Dayia navicula*, *Leptaena rhomboidalis*, *Sphaerirhynchia wilsoni*, *Strophonella euglypha*, *S. funiculata*, bryozoans, *Michelinoceras tenuiannulatum*, *Cornulites serpularius*, crinoid columnals and *Monograptus* sp.

Following the river bank north-eastwards, an extensive old quarry in Upper Bringewood Beds may be seen on the opposite side of the river. A typical "Aymes-try Limestone" facies is exposed also (43067313) between the dip arrow and Bow

Bridge (locality (45)) on the eastern side of the river. There are bands of *Conchidium knighti* and *Favosites* is common. Also present are solitary corals, *Stromatopora* sp., bryozoans, *Atrypa reticularis*, *Brachyprion* sp. nov., *Isorthis orbicularis*, *Leptaena rhomboidalis*, *Sphaerirhynchia wilsoni*, *Strophonella euglypha*, *Cypricardinia planulata*, gastropods, *Kionoceras angulatum* and crinoid columnals.

Lower Leintwardine Beds are not well exposed in this section but at locality (46) (43117320) in the field below the track from Bow Bridge and under a tree a small exposure shows some of the fossils typical of the division. The following were collected here: *Camarotoechia nucula*, *Chonetes lepismus*, *Isorthis orbicularis*, *Dayia navicula*, *Sphaerirhynchia wilsoni*, *Lingula* sp., bryozoans, *Slava interrupta*, *Calymene* sp. and graptolite fragments.

A rising track leads southwards up the steep slope from the main track near locality (46) and branches north-eastwards to locality (47) (43197316). Here the Upper Leintwardine Beds, as is characteristic in the western part of the district, are indicated by thin biscuity bands with *Chonetoidea grayi* and *Neobeyrichia lauensis*, which can be located in poor exposures in the trackside just west of the bend. A better exposure (locality (48)) is a small old quarry (43297312) in the bracken covered ground to the south of the track. Here the uppermost 3 ft. of strata have yielded *Chonetoidea grayi* and *Neobeyrichia lauensis*.

Returning to the river bank, a clear track leads north-eastwards to Hay Mill, where an old quarry, locality (49) (43457352), shows typical Lower Whitcliffe Beds with their irregular, thickly flaggy to massive bedding and comparatively sparse fauna. The steepest and most impressive part of Downton Gorge coincides with the outcrop of the Lower Whitcliffe Beds and can be followed by a rocky pathway close to the eastern bank of the river. Typical Lower Whitcliffe Beds are exposed (locality (50)) along this pathway, though much of the material is loose. Here a representative Lower Whitcliffe fauna includes *Camarotoechia nucula* and *Fuchsella amygdalina* (both common), *Serpulites longissimus* and *Michelinoceras imbricatum* (both fairly common), together with *Protochonetes ludloviensis*, *Michelinoceras bullatum* and *Michelinoceras ibex*. At locality (51) (43987400) is a river cliff reached by an old walled tunnel, where the typically massive bedding of the Lower Whitcliffe Beds is seen again. Here is the approximate place at which the axis of the Downton Syncline crosses the river (see Whitaker, 1962) and the effect of the north-easterly plunge is apparent. Higher above the river the quarried crags (locality (52) (44027390)) are of more thinly bedded, somewhat yellowish weathered, Upper Whitcliffe Beds with their characteristic and common fauna. This includes especially *Camarotoechia nucula*, *Protochonetes ludloviensis* and *Salopina lunata*, together with the ostracod *Beyrichia kloedeni* var. *torosa*. If the long line of old quarries is followed south-eastwards away from the river the succession is descended again. At the south-eastern end (locality (53) (44107367)) may be seen the group of slump structures described in detail by Whitaker (1962) from a locality on the opposite side of the river and marking the top of the Lower Whitcliffe Beds. Further north-eastwards the riverside path passes old quarries (localities (54) and (55)) in fossiliferous Upper Whitcliffe Beds, which show an east-south-easterly dip representing the north-western limb of the Downton Syncline.

At locality (56) (44427425) where the path nears Downton Castle Bridge the uppermost Whitcliffe Beds are exposed in a small "cliff" above the path. These are the "*Spirifer elevata* shales" of Elles & Slater (1906 : 208) and this small brachiopod, now renamed *Howellella elegans*, is common. As these authors noted, there is also a thin "biscuity" band (actually approximately 8 ft. below the Ludlow Bone Bed, see locality (57)) containing abundant casts of *Craniops implicata*. A similar band is to be found in certain other Welsh Borderland areas in the uppermost part of the Ludlovian (Holland, 1962). The fauna collected from this prolific locality is as follows: bryozoans, *Camarotoechia nucula*, *Protochonetes ludloviensis* (both very common), *Craniops implicata*, *Howellella elegans*, *Lingula* sp., *Salopina lunata* (very common), *Fuchsella amygdalina*, *Goniophora cymbaeformis*, *Modiolopsis complanata*, *Pteronitella retroflexa*, *Pterinea* sp., *Loxonema* sp., *Michelinoceras imbricatum*, *Cornulites serpularius*, *Serpulites longissimus* and *Beyrichia kloedeni* var. *torosa*.

On the south-west side of the main track leading from Downton Castle Bridge an old quarry, locality (57) (44497427), shows the lowest Downtonian immediately succeeding the Whitcliffe Beds which are exposed round the corner at locality (56). The Ludlow Bone Bed is found in slightly disturbed ground at the north-western end of the quarry and about 4 ft. above present road level. About 2 ft. higher, still in the slightly disturbed bank, are *Platyschisma helicites* beds with some bony material (Downton Bone Bed). Above, and exposed in the main part of the old quarry, is typical Downton Castle Sandstone. This whole section was described by Elles & Slater (1906 : 208, 209). Within the Downton Castle Sandstone 4 ft. of massive yellowish siltstones are succeeded by a foot and a half of carbonaceous siltstones, and these in turn by some 7 ft. of laminated, false bedded, yellowish siltstones.

As shown in Text-fig. 10 a fault runs south-eastwards parallel with the track. Beyond this and along the riverside path there are exposures of Red Downtonian rocks, red weathering, greenish siltstones and micaceous sandstones, together with some red "marls". These beds are better and more typically displayed in the stream section running north-north-westwards through a wood towards the Teme at 44747442, about 300 yards from Downton Castle Bridge.

Further exposures of Downtonian strata, including the Temeside Shales, may be seen by following the track south-eastwards from the bridge and taking the branch south-westwards which leads into a large field on the dip slope. At locality (58) (44427402), some 60 yards beyond a gate, fossiliferous Upper Whitcliffe Beds, poorly exposed in the track surface, are succeeded north-eastwards by basal Downtonian beds. Specimens of the Downton Bone Bed, with its associated *Platyschisma helicites* and *Modiolopsis complanata* (J. de C. Sowerby) were collected here. Locality (59) (44497409), further to the north-east, shows bedding planes of Downton Castle Sandstone in the track below the gate. On the north side of the exposure, at the eastern end, typical blocky greenish siltstones of the Temeside Shales are seen in the bank, overlying the Downton Castle Sandstone.

(2) Burrington

Near Burrington Farm (44357240), Wenlock Shales are exposed by the lane leading

eastwards (locality (60)), as well as in the steep bank on the eastern side of the main lane leading northwards (locality (61)). Limestone ribs and nodules are still relatively scarce and the lithology is typical of the Wenlock Shales (see p. 103). There is calcite veining hereabouts associated with the fault shown on the sketch-map (Text-fig. 10). The rather fragmentary small brachiopods here include *Dicoelosia biloba*. Other fossils collected are orthoconic nautiloids, *Dalmanites myops* and *Monograptus vulgaris*.

At locality (62) (44257253) opposite a field boundary the base of the Wenlock Limestone is marked by a sudden increase in ribs of flaggy limestone, which above this locality alternate persistently with the shales. Above the boundary and round the bend (locality (64) (44177257)) the lane surface shows more or less continuous exposures in the alternating flaggy limestones and shales, giving the effect of a series of short stone steps. This lower flaggy part of the Wenlock Limestone is seen also in an old quarry, locality (63) (44257255), where the flaggy limestones stand out conspicuously from the face or are picked out by lichen. These beds are very poorly fossiliferous with only a few brachiopod and graptolite fragments.

Further north-eastwards the lane crosses a fault and beyond this at locality (65) an old quarry (44377266) shows the upper nodular part of the Wenlock Limestone. The fauna is still sparse but includes the following: *Stromatopora carteri*, *Atrypa reticularis*, *Leptaena rhomboidalis*, *Resserella elegantula*, *Strophonella euglypha*, *Calmene* sp., *Proetus* sp., *Hemsiella maccoyana* and crinoid columnals.

Continuing along the lane, a small exposure (44507277) under the hedge before the barn (locality (66)) shows the blocky, irregularly bedded Lower Elton Beds with their characteristic greenish colour and white shell fragments. There are hard limestone bands and nodules. The fauna includes *Camarotoechia nucula*, "*Dalmanella*" sp., *Lingula* sp., *Resserella elegantula*, *Calymene* sp., crinoid columnals and numerous brachiopod fragments. The Lower Elton Beds are exposed again at locality (67) (44537278), where a small stream emerges northwards from under the lane.

From the bend in the lane at locality (64), already referred to, a track branches northwards. At first (68) (44147263) there are exposures of the flaggy lower part of the Wenlock Limestone but down the track these are followed by nodular limestones. From here the stream section along Nunfield Gutter is easily reached and can be followed to the Teme at Owney Cottage. Locality (69) (43897278) is the standard section for the base of the Middle Elton Beds and the detailed faunal and lithological changes across this boundary are described in detail for this locality on p. 107. Further westwards the stream meanders along the boundary and there are numerous other exposures, the best of which are indicated on the map. Localities (70), (71) and (73) are of typical Lower Elton Beds while the better bedded Middle Elton Beds are seen at localities (72), (74) and (75).

The track north-westwards from locality (68) crosses Nunfield Gutter (44027279) and ascends obliquely the scarp slope of Middle and Upper Elton Beds. The standard section for the base of the Upper Elton Beds (locality (76) (43677283)) is along this track and is described in detail on pp. 110-111.

Finally, from locality (68) another branch of the track runs northwards and can

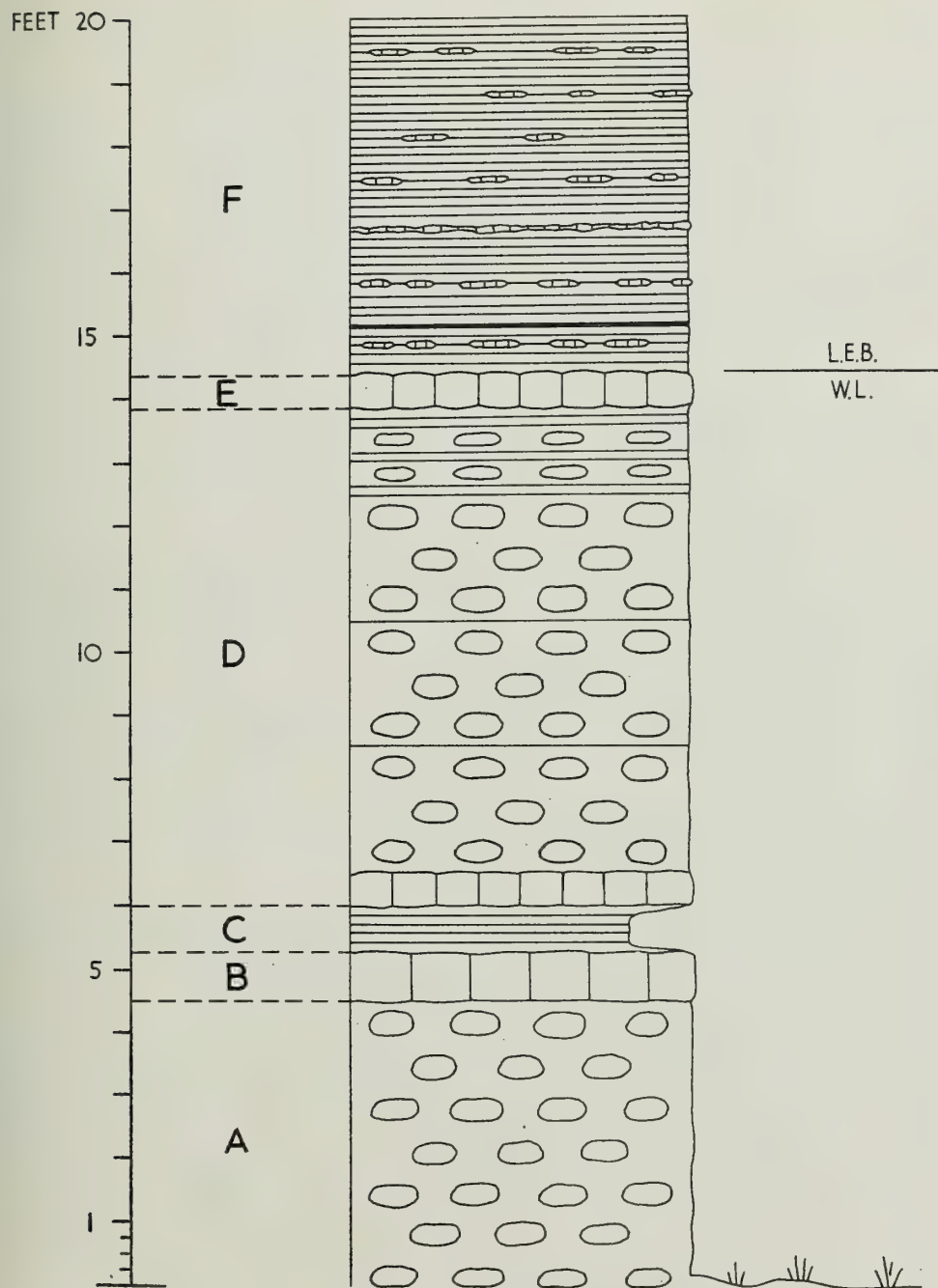


FIG. 11. Diagrammatic section showing the position of the boundary between the Wenlockian and Ludlovian Series in the quarry at Pitch Coppice (for explanation see pp. 139-141).

be followed as shown on the map to the steep wooded scarp of Burrington Hays, where a long old quarry (locality (77) (43757307) shows Upper Bringewood Beds succeeded by Lower Leintwardine Beds. The Upper Bringewood Beds are somewhat nodular, irregularly bedded limestones with the diagnostic *Conchidium knighti*. Also present are: *Atrypa reticularis*, *Dayia navicula*, *Leptaena rhomboidalis*, *Sphaerirhynchia wilsoni*, bryozoa and crinoid columnals. These limestones are succeeded sharply (contrast the standard section at Sunnyhill Quarry, locality (30), pp. 141-145) by about 9 ft. of Lower Leintwardine Beds, which are relatively soft, well bedded, thinly flaggy and shaly, calcareous siltstones. A rich brachiopod fauna includes *Atrypa reticularis*, *Camarotoechia nucula*, *Chonetes lepisma*, *Dayia navicula* (very common in bands), *Isorthis orbicularis*, *Lingula lata*, and *Sphaerirhynchia wilsoni*, together with bryozoans and *Fuchsella amygdalina*. The absence of *Conchidium knighti* and abundance of *Chonetes lepisma* and *Dayia navicula* are noteworthy, as is the appearance of *Fuchsella amygdalina*. There are thin rottenstone bands crowded with *Dayia navicula*.

V. STRUCTURE

The regional trend of the south-easterly dipping Silurian rocks from Much Wenlock through Craven Arms is interrupted by the Ludlow Anticline and the line of faulting to the south of it. This anomalous fold, like the Brecon Anticline which breaks the regional pattern further to the south, may well be related to important fracturing within the Pre-Cambrian basement.

The Ludlow Anticline plunges to the east-north-east at about 5 degrees and is asymmetrical with a steeper northern limb. Within the northern limb dips of 30 to 40 degrees occur to the west near Downton Gorge, while further east the dip falls to 10 to 20 degrees. The dip on the southern limb is about 10 degrees. The approximate line of the "axis" of the anticline is shown in the sketch-map of the Wigmore Road (Text-fig. 8) and is referred to in the detailed description of the Whitcliffe on p. 125.

The complementary Downton Syncline to the north-west has been described by Whitaker (1962). Its axis lies mainly to the west of the River Teme, but at the two bends to the north of Bow Bridge and near Hay Mill and along the reach above Downton Castle Bridge it lies just to the east of the river.

Faulting in the Ludlow district is in two main directions: west-south-west to east-north-east and north-west to south-east, that is, parallel and approximately perpendicular to the fold axis. The field evidence is inadequate to suggest the type of faulting.

Three more or less parallel small faults to the north and east of Burrington (see Map) affect the outcrop and topographical expression of the Wenlock Limestone. A fourth, at right angles to these and north of them, is responsible for a shift in the main Ludlovian scarp feature, causing a deep oblique valley below Burrington Hays. On the opposite, south-eastern side of the anticlinal axis two small faults near Aston again affect the Wenlock Limestone.

Of greater magnitude are the two faults along the northern margin of the district,

which in places separate the Ludlovian and Downtonian. The western fault which crosses the Teme at Downton Castle Bridge combines the two fault directions already referred to. Whitaker (1962) has traced this fault north-westwards into the Leintwardine district. Near the bridge it has a north-easterly downthrow of at least 170 ft., bringing Red Downtonian against uppermost Ludlovian. About a mile to the east there is evidence that the throw has diminished. At locality 139 (see Appendix 1, p. 166), for example, the fault is seen between uppermost Ludlovian and Downton Castle Sandstone. Only 8 ft. of the latter is present under the Temeside Shales. Thus the northerly downthrow is here about 40 ft. A short distance to the east the fault dies away.

The second of the two northern boundary faults can be traced from the north of Ludlow Castle westwards for about a mile and a half parallel to the anticlinal axis, and makes a steep scarp feature. At its maximum northerly downthrow of about 270 ft., the base of the Whitcliffe Beds is in contact with the base of the Red Downtonian. On the folding map, over two miles of unfaulted boundary between Ludlovian and Downtonian connects the faults described above. This interpretation differs from that of Elles & Slater (1906), in which there is a single northern boundary fault.

Moving southwards from Ludlow (see Map), a pair of north-west to south-east faults is shown near Overton. Evidence for the longer one along the Mary Knoll valley is given on p. 131.

Finally, the three faults at the south-eastern limit of the district are but a small part of a line of faulting of regional significance which extends east-north-eastwards through Titterstone Cleve Hill to the Forest of Wyre Coalfield and west-south-westwards to join the Church Stretton Disturbance near Presteigne. The southernmost fault is the important one in this group of three and has a downthrow to the north of about 200 ft.

From the evidence obtained within the Ludlow district itself it can only be said that the age of the movements which produced the Ludlow Anticline and its associated faults is post-Downtonian. Ball & Dineley (1961) have given evidence from the Cleve Hills that the main form of these structures was set by post-Dittonian pre-Farlovian movements, but that there were later movements at the end of the Farlovian and during the Carboniferous.

VI. STAGES OF THE LUDLOVIAN

As explained in Section II, the four stages into which the Ludlovian Series is here divided have been defined by means of standard sections for their bases. Detailed descriptions of these four standard sections are included in the following pages. In order to delimit the Ludlovian Series a standard section for the base of the Downtonian Stage of the Lower Old Red Sandstone Series is then described.

(a) *Base of the Eltonian Stage*

The standard section for the base of the Ludlovian Series, Eltonian Stage, and Lower Elton Beds is in the old quarry (47267301) in Pitch Coppice, on the south side of the Ludlow-Wigmore road about one mile north-east of Aston Church. The

quarry is shown on the sketch-map (Text-fig. 8, locality (16)) and a diagrammatic section of the face is given in Text-fig. 11. Nearly 15 ft. of Wenlock Limestone is capped by several feet of Lower Elton Beds. The latter are accessible at both the western and eastern ends of the quarry face and are exposed also in a bank above the north-western corner of the quarry.

The Lower Elton Beds, though rich in broken shell fragments, are poor in identifiable fossils. There is however a clear lithological change from the Wenlock Limestone below, at which the boundary is defined. The uppermost Wenlock Limestone here, as elsewhere in the district, is nodular in character and the succeeding Lower Elton Beds are typical soft, olive, shaly siltstones.

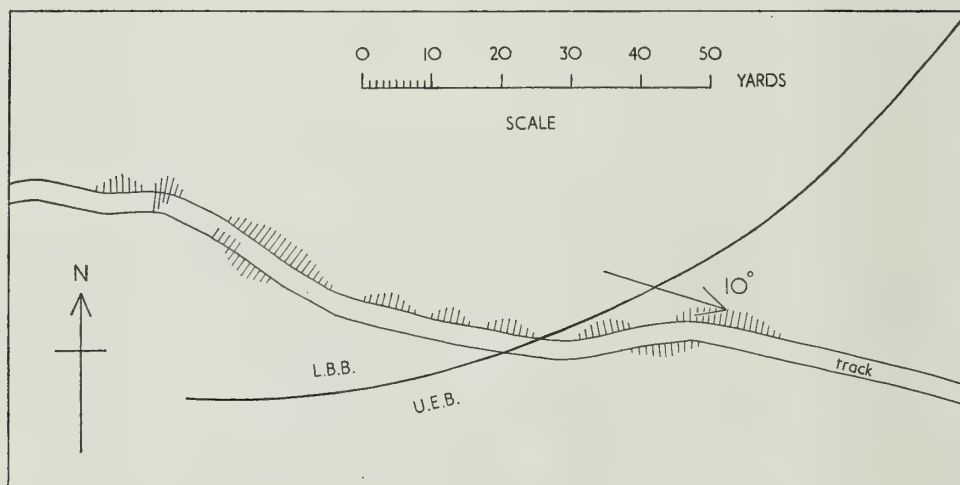


FIG. 12. Plan of the standard locality in Mary Knoll Valley for the boundary between the Eltonian and Bringewoodian Stages (for explanation see opposite).

Details of the lithological changes near the boundary as shown in Text-fig. 11 are as follows: the lower part of the quarry face (A) is of massive, nodular, grey limestone capped by (B) a hard ledge of limestone 8 to 10 in. thick. Above this are 8 to 9 in. of shales (C) (similar to the Wenlock Shales) which have been weathered back to a conspicuous hollow along the face. Above this are nodular limestones (D) almost 8 ft. thick with some thin shaly partings especially towards the top. Completing the Wenlock Limestone is a cap (E) of 5 to 7 in. of hard limestone. The succeeding Eltonian (F) is of soft, olive, calcareous shaly siltstones with white shell fragments, broken by irregular thin bands and lenses of hard limestone. There is a thin clay band 9 in. from the base.

From the Wenlock Limestone in this quarry, the following have been recorded: *Favosites asper*, *Heliolites interstinctus*, *Thecia grayana*, solitary coral, bryozoans, *Atrypa reticularis*, *Gypidula galeata*, *Leptaena rhomboidalis*, *Resserella elegantula*, *Sphaerirhynchia wilsoni*, *Strophonella euglypha*, *Poleumita discors*, *Lituites ibex*, crinoid columnals, *Dalmanites myops*, *Hemsiella maccoyana* and *Primitia* sp.

Apart from their abundant shell fragments, the Lower Elton Beds have yielded *Atrypa reticularis*, *Chonetes minimus*, *Leptaena rhomboidalis*, *Resserella elegantula*, *Calymene* sp., bryozoans, crinoid columnals and ostracod fragments.

The question of the graptolite zones about the Wenlockian-Ludlovian boundary (Das Gupta, 1932; Pocock, Wedd & Robertson, 1938; Whittard, 1952) remains difficult in that the position of the base of the *Monograptus vulgaris* Zone in relation to the Wenlock Limestone is not known. In the present investigation the only relevant graptolite evidence is the occurrence in the higher beds of the Wenlock Shales of *Gothograptus nassa*, *Monograptus dubius* and *M. vulgaris*, of which the second is the least rare. Such an assemblage is not inconsistent with either the *Cyrtograptus lundgreni* Zone or *Monograptus vulgaris* Zone but is perhaps more characteristic of the higher part of the former. The problem of the graptolite sequence in areas where the Wenlock Limestone is developed might be solved by prolonged collecting throughout the Welsh Borderland but the rarity of graptolites at this level in the shelf facies would make this a most difficult task. In any event it is desirable that at the standard locality the Wenlock Limestone should be within the Wenlockian and the Ludlovian (Eltonian) should begin above it.

(b) *Base of the Bringewoodian Stage*

The standard locality for the base of the Bringewoodian Stage is on the western slopes of the Mary Knoll Valley and is a track section (map reference 48737292 and Text-fig. 12). It is reached by following the Forestry Commission road shown on Text-fig. 9 north-westwards for a further 375 yards beyond the edge of that map until a tributary stream is crossed and two paths branch off to the left. About 150 yards along the ascending track the standard section commences. It is the standard for the base of the Lower Bringewood Beds and for the base of the Bringewoodian Stage.

The junction is not clearly defined but is perhaps most accurately described as a rapid transition in both lithology and fauna. The Upper Elton Beds are somewhat calcareous, smoothly bedded, flaggy and shaly siltstones with occasional hard flaggy limestone bands; *Monograptus tumescens* is abundant in the flaggy bands which break off in large pieces. Shelly fossils are not common apart from *Chonetes lepisma* but *Dalmanites myops* occurs. The Lower Bringewood Beds here are not yet typical but are slightly more thickly and irregularly bedded than the Upper Elton Beds, with a notable absence of the flaggy limestones. It is less easy to collect slabs of rock. These beds were probably originally more calcareous than the Upper Elton Beds but are now decalcified to a brownish colour. *Monograptus tumescens* is still fairly common in the basal beds but shelly fossils become more abundant particularly *Brachyprion* sp. nov. *Chonetes lepisma* is very common; *Dalmanites myops*, *Camarotoechia nucula*, *Dayia navicula*, bryozoans and ostracods also occur. The position of the boundary is shown on the map (Text-fig. 12).

(c) *Base of the Leintwardinian Stage*

The standard section for the base of the Leintwardinian Stage and also therefore for the base of the Lower Leintwardine Beds is on the north-west face of Sunnyhill

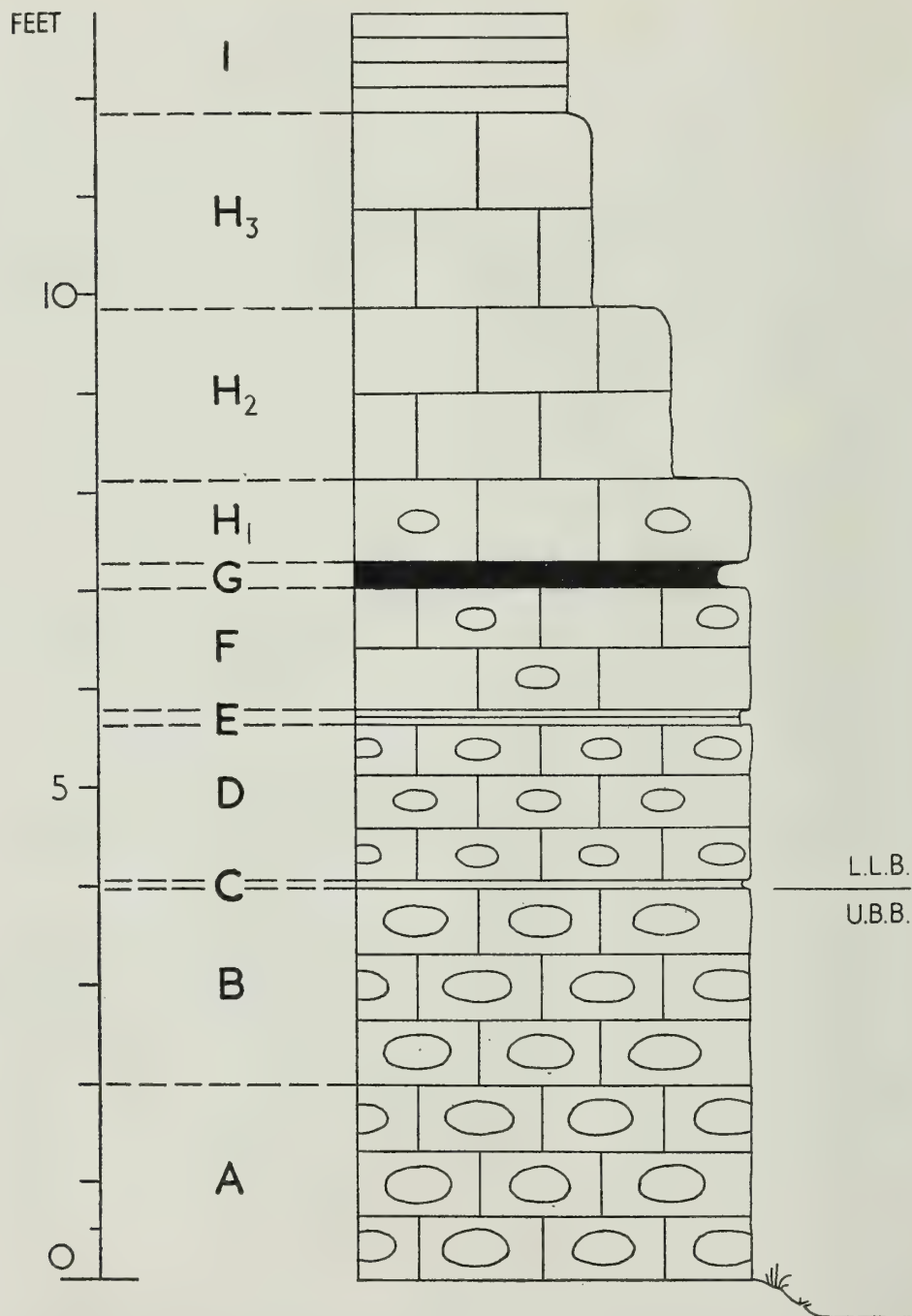


FIG. 13. Diagrammatic section showing the position of the boundary between the Bringewoodian and Leintwardinian Stages at Sunnyhill Quarry (for explanation see opposite).

Quarry (map reference 49537255, map, Text-fig. 9). A diagrammatic section across the boundary is shown in Text-fig. 13. On first examination this quarry might appear to be entirely in the Aymestry Limestone of the earlier classification (and therefore probably in the Upper Bringewood Beds of this classification). The fauna of most of the strata, however, is unmistakably that of the Mocktree Shales (i.e. Lower Leintwardine Beds of this classification). In this eastern part of the area the calcareous phase in the middle of the Ludlovian persists into the Leintwardinian Stage. The quarry mainly shows thinly bedded calcareous siltstones but the clean vertical joint faces encourage the illusion of massive limestones. If the Geological Survey usage of the term Aymestry Limestone as a rock-stratigraphical unit is followed then this quarry might be mapped as Aymestry Limestone, but in the *Dayia navicula* Zone not the *Conchidium knighti* Zone of Elles & Slater (1906). The lowest beds are seen in the west close to the road and consist of 4 ft. of nodular limestones and calcareous siltstones with uneven partings. In the lower 2 ft. (A in Text-fig. 13) such typical Upper Bringewood fossils as *Conchidium knighti*, *Strophonella euglypha*, *Rhabdocyclus* and small trochoid corals have been found. Of forms which range above, *Atrypa reticularis* is abundant, crinoid columnals are common and *Camarotoechia nucula*, *Howellella elegans*, *Isorthis orbicularis*, *Leptaena rhomboidalis* and *Sphaerirhynchia wilsoni* are present. In the upper 2 ft. (B), *Atrypa reticularis* and *Isorthis orbicularis* are the dominant fossils. Crinoid columnals are also common and *Camarotoechia nucula*, *Dayia navicula*, *Sphaerirhynchia wilsoni* and *Monograptus* sp. also occur.

Dayia navicula occurs in the Lower Bringewood Beds and the *Monograptus* is unidentifiable so that in spite of no diagnostic Bringewood fossils being found in section B it has been decided not to separate the latter from A, with which it is in lithological continuity. The boundary has therefore been taken at the base of the $\frac{1}{4}$ -in. shale parting C, although the fauna in the succeeding 8 ft. is substantially similar to that in B. D consists of 19 in. of more thinly bedded nodular limestones and calcareous siltstones. E is a 2-in. wide shale band overlain by F, 15 in. of massive, somewhat nodular limestone. There succeeds a prominent 3-in. band of soft clay (G) which can be traced also between the two lowest ledges of limestone below the main face, although here the clay band is hidden by a thick growth of grass. Above, in H, there follows $4\frac{1}{2}$ ft. of flaggy to massive, silty limestone, somewhat nodular especially in the lower part. Below the main face of the quarry these limestones form the two upper ledges (10 in. and 21 in.) plus 2 ft. of rock before the beds at I.

The general faunal characteristics of the 8 ft. of beds D to H inclusive are as follows: common fossils are *Atrypa reticularis*, *Camarotoechia nucula*, *Isorthis orbicularis* and crinoid columnals; also present are *Chonetes lepisma*, *Dayia navicula*, *Shaleria ornatella*, *Sphaerirhynchia wilsoni*, *Craniops implicata*, *Lingula lewisi*, *Orbiculoidea rugata*, *Slava interrupta* and *Beyrichia* sp. One specimen which may be a *Gypidula* was found in the top of H and pentagonal crinoid columnals occur sparsely in F and H₁. In the succeeding beds (I) there is a distinct lithological change to thinly flaggy, even shaly, calcareous siltstones with frequent curved joint surfaces; *Chonetes lepisma* and *Dayia navicula* now appear in some abundance.

FEET

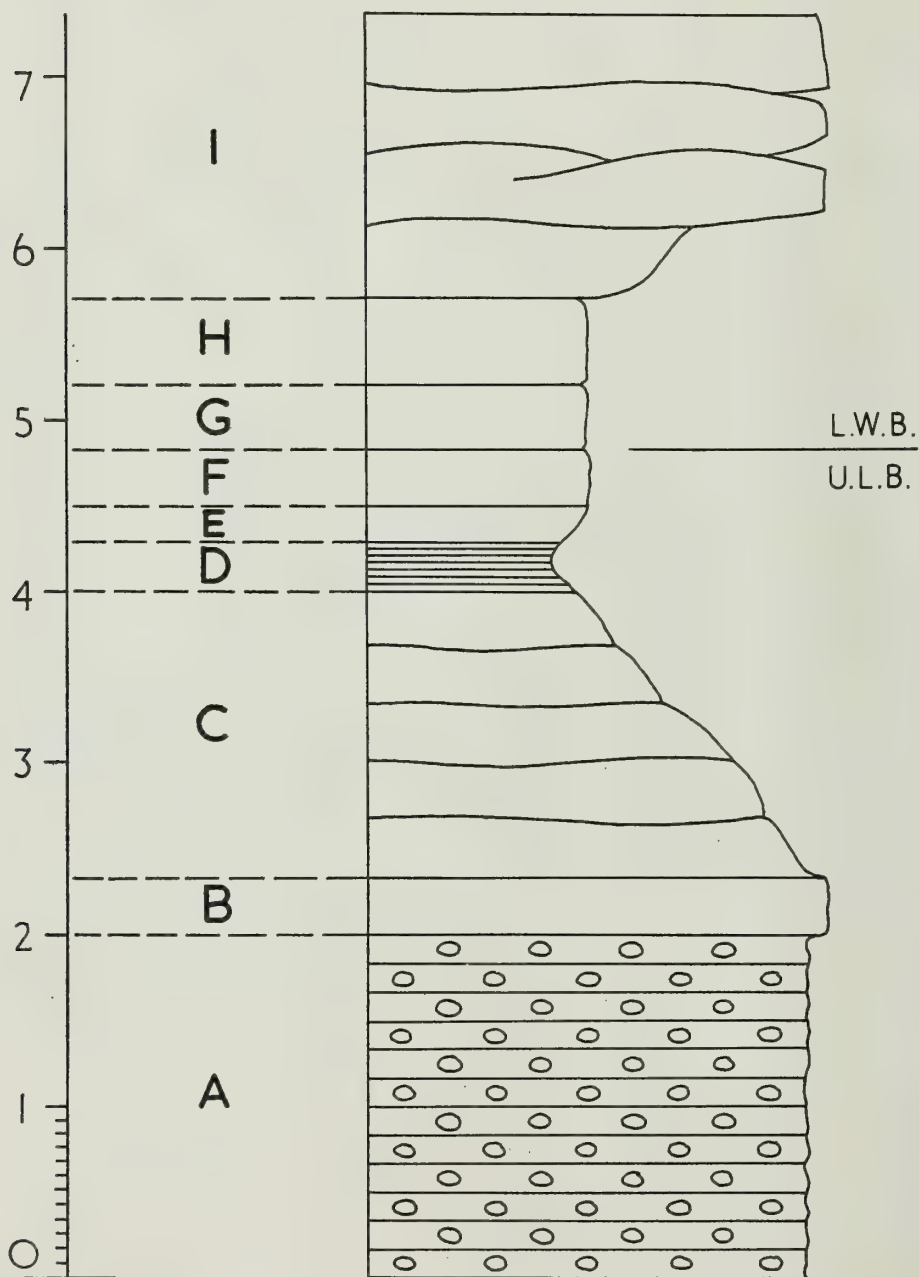


FIG. 14. Diagrammatic section showing the position of the boundary between the Leintwardinian and Whitcliffian Stages on the Whitcliffe (for explanation see opposite).

Although this change would seem to offer a suitable boundary in this particular quarry it is considered that the disappearance of the Bringewood forms is of more significance in wider correlation and therefore a more suitable criterion for a stage boundary. For this reason the shale parting C has been preferred.

(d) *Base of the Whitcliffian Stage*

The standard section for the base of the Whitcliffian Stage and for the base of the Lower Whitcliffe Beds is at locality (3) on the sketch-map of the Whitcliffe (Text-fig. 7). The map reference is 50717428 and the line Y indicates the position of the section in the sketch of the cliff (Text-fig. 4). A vertical section across the boundary is given in Text-fig. 14 and a photograph in Plate 2.

At the top of the slope rising from the river bank the cliff starts with about 5 ft. of flaggy calcareous siltstones, conspicuously honeycombed, of which only the top 2 ft. are shown as A in the diagram (Text-fig. 14). These are clearly Upper Leintwardine Beds and contain *Atrypa reticularis*, *Camarotoechia nucula* (common), *Protochonetes ludloviensis*, *Chonetoida grayi*, "*Dalmanella*" sp., *Leptaena rhomboidalis*, *Shaleria ornatella*, *Calymene neointermedia*, *Encrinurus* sp., proetid trilobite, *Pterinea nupera*, *Pteronitella retroflexa*, *Michelinoceras bullatum*, *Kionoceras angulatum*, *Bucanopsis expansus*, *Serpulites longissimus* and bryozoans. Bed B is an easily identifiable siltstone cap about 3–4½ in. thick (indicated by the matchbox in Plate 2) and includes a layer fairly rich in biotite flakes; fossils are not common but *Atrypa reticularis*, *Camarotoechia nucula*, *Leptaena rhomboidalis*, *Fuchsella amygdalina*, *Serpulites longissimus*, bryozoans and crinoid columnals have been found. The succeeding 20 in. of siltstones (C) are more thickly and irregularly bedded and less calcareous; lithologically they resemble the Lower Whitcliffe Beds but the fairly common occurrence of *Shaleria ornatella* and the presence of *Monograptus* cf. *leintwardinensis* indicate the Upper Leintwardine Beds. Other fossils are *Camarotoechia nucula* (large form common), *Protochonetes ludloviensis* (often small), *Dayia navicula*, *Orbiculoidea rugata*, *Salopina lunata*, *Fuchsella amygdalina*, *Pteronitella retroflexa*, *Michelinoceras bullatum*, *Bembexia lloydi*, *Serpulites longissimus* and bryozoans. Several seams of shell fragments occur. D comprises 3½ in. of shale overlain by 2–2½ in. of calcareous siltstone (E); these beds have yielded *Camarotoechia nucula*, *Protochonetes ludloviensis*, *Dayia navicula*, *Lingula lewisi*, *Fuchsella amygdalina*, *Pteronitella retroflexa*, *Kionoceras angulatum* and *Cyclonema coralli*. F is a very fossiliferous calcareous siltstone 3½ to 4 in. thick and the abundance of *Chonetoida grayi* is taken as a definite indication of Upper Leintwardine Beds. *Shaleria ornatella* also occurs, together with *Camarotoechia nucula*, *Protochonetes ludloviensis*, *Craniops implicata*, *Dayia navicula*, *Michelinoceras* sp., *Kionoceras angulatum*, *Serpulites longissimus* and *Bythocypris* sp.

The base of the succeeding bed G, a poorly fossiliferous calcareous siltstone 4–4½ in. thick (indicated by the head of the upper hammer in Plate 2) is defined as the base of the Lower Whitcliffe Beds and of the Whitcliffian Stage. Above is a 6 in. band of shelly limestone (H) and although fossils are common, there is now no sign of the characteristic Leintwardinian fauna. *Camarotoechia nucula*, *Protochonetes*

ludloviensis and *Dayia navicula* occur most frequently. The overhanging strata in I are typical thickly and irregularly bedded siltstones of the Lower Whitcliffe Beds. *Camarotoechia nucula* (large form) and *Fuchsella amygdalina* are common; *Protochonetes ludloviensis* (often small), *Michelinoceras imbricatum* and *Bembexia lloydi* also occur.

The total thickness of the Upper Leintwardine Beds in this standard section on the Whitcliffe is 18 ft.

(e) *Base of the Downtonian Stage*

The upper limit of the Whitcliffian Stage, and therefore of the Ludlovian Series, is taken at the base of the Ludlow Bone Bed in the "Ludford Lane" section (51237413). This is shown as locality (7) on the sketch-map of the Whitcliffe (Text-fig. 7). This horizon is here *defined* as the base of the Downtonian Stage and the Lower Old Red Sandstone Series.

The Upper Whitcliffe Beds are grey, calcareous, flaggy siltstones with *Camarotoechia nucula*, *Protochonetes ludloviensis*, *Howellella elegans* and *Salopina lunata* common. Above the Ludlow Bone Bed, the siltstones of the Downton Castle Sandstone formation are somewhat coarser than those of the Upper Whitcliffe Beds. In composition they are more micaceous and less calcareous, whilst in colour, yellowish and greenish tints are more common. Faunally the formation is characterized by the occurrence of *Lingula minima* J. de C. Sowerby, *Kloedenia wilckensiana* (Jones), *Modiolopsis complanata*, *Platyschisma helicites*, eurypterids, plants, and fish remains in thin layers. The 3 ft. of strata above the Ludlow Bone Bed are poorly fossiliferous. Above this, and up to 6 ft. above the Bone Bed where the yellowish false-bedded sandstones begin, the fauna is well developed with several ostracod bands and common *Platyschisma helicites*.

VII. CORRELATION

(a) *Wenlockian Series*

As no faunal divisions of the shelf Wenlockian Series based on shelly fossils have yet been proposed, only a lithological correlation of the formations are possible. The Wenlock Shales of the Ludlow district are similar to those below Wenlock Edge and in the inliers of Woolhope, Malvern and May Hill. The succeeding flaggy limestones and shales are quarried; they form a fairly strong feature and have therefore been classified here as Wenlock Limestone. Only the highest 50 ft. of nodular beds, however, are sufficiently calcareous and fossiliferous to invite comparison with the so-called typical Wenlock Limestone of Wenlock Edge and Wren's Nest. As the Ludlow area is closer to the basin facies it may well be that the lower flaggy division is a more argillaceous lateral equivalent of the lower part of the Wenlock Limestone elsewhere, although lithologically these strata show some resemblance to the Tickwood Beds, the uppermost division of the Wenlock Shales in the type area.

The problem of the definition of the top of the Wenlock Limestone is discussed on pp. 140-141.

(b) *Ludlovian Series*

Various authors in recent years (Lawson, 1955; Walmsley, 1959; Holland, 1959; Squirrell & Tucker, 1960) have made tentative correlations between the areas they have mapped and the Ludlow district. These correlations are now reconsidered in terms of the revised classification which includes the two widespread and faunally distinctive divisions, the Lower Bringewood Beds and the Upper Leintwardine Beds, not recognized by earlier writers on the Ludlow area. The detailed reasons for the preferred correlations are not repeated from these recent papers.

In the chart (Table II), firm lines in columns 5, 6, 7, 8 and 9 indicate a fairly certain correlation with the biostratigraphical divisions at Ludlow. Firm lines in column 10 (Generalized Basin Succession) suggest a reliable correlation with the Ludlow classification in column 4. In columns 11-16 firm lines indicate a fairly certain correlation with the basin divisions of column 10. Column 17 gives the graptolite zones introduced by Wood (1900) and modified slightly by Alexander (1936). The units in columns 5 to 17 are all essentially biostratigraphical (or faunal) divisions and their correlation with the time-rock classification into stages (column 3) depends on the reliability of certain fossils as time indices. At present, no better criteria are available. Most reliance has been placed on the graptolites but as they are not common in the shelf facies and are absent altogether from the higher beds it is necessary to make cautious use of the shelly faunas (see Lawson, 1960). Certain trilobites (e.g. *Calymene neointermedia*) and ostracods (e.g. *Neobeyrichia lauensis*) have a relatively restricted range and show some independence of facies changes; these are the most valuable of the shelly fossils for correlation. The brachiopods were more influenced by changes in the conditions of sedimentation so that even the distinctive assemblages can only be trusted within limits. As explained more fully by Lawson (1960: 123) it is the disappearance of these successive faunas that is of most significance, although only in the British area. There are a few brachiopod species, however, which do disappear at approximately the same stratigraphical level (using graptolite zones as criteria) both within and beyond the British area (e.g. *Dicoelosia biloba*, *Skenidioides lewisi*, *Strophonella euglypha*, *S. funiculata*). The mollusca, corals and bryozoans, in spite of their greater dependence on environment, are helpful in correlation over short distances particularly when considered together with the more reliable fossils in the assemblages. The detailed application of these principles is seen in the papers on particular areas listed above and in a general paper on the Ludlovian rocks of the Welsh Borderland by Lawson and others (1956).

(i) *Shelf Facies*

The general characteristics of this development have recently been summarized by Lawson (1960: 114) and will not be repeated here.

(1) *Leintwardine* (Column 5)

The succession in this area immediately west of the Ludlow district has recently been described by Whitaker (1962). There is a greater total thickness of strata and the sediments and faunas show distinct affinities with those of the basin facies. It

is therefore of particular interest to note the thick development of the shallow-water, calcareous Upper Bringewood Beds (Aymestry Limestone facies) and the presence of a marked unconformity along the lines of submarine channels eroded in Leintwardinian times.

(2) *Usk* (Column 6)

It is now proposed that the names of the biostratigraphical divisions at Ludlow be applied to equivalent divisions in the shelf inliers. The local names need only be used where correlation is uncertain. For example, the Lower Llanbadoc Beds can now be referred to as the Upper Bringewood Beds of Usk. The rock-stratigraphical term Aymestry Limestone, which many geologists might at first prefer, can be used only for the Lower Llanbadoc Beds in the east of the inlier. To the west these strata, although still resistant enough to form a feature, are not sufficiently calcareous to justify the name limestone.

In this inlier (Walmsley, 1959) there is a complete succession of comparable thickness to that at Ludlow and correlation is straightforward apart from the Elton Beds. The Lower Elton Beds compare with the basal Lower Forest Beds and the Upper Elton Beds are perhaps indicated by the rare occurrence of *Monograptus* cf. *tumescens* in the otherwise shelly upper part of the Lower Forest Beds. The Elton Beds and the Lower Forest Beds are of similar thickness and it seems likely that the Middle Elton Beds are here represented by the middle of the Lower Forest Beds in a non-graptolitic development. The twofold division of the Whitcliffe Beds has not been recognized at Usk but the highest Ludlovian strata in the inlier are distinguished by the abundance of *Loxonema* [*Holopella*], as at Builth.

(3) *Woolhope* (Column 7)

Squirrell & Tucker (1960 : 156) correlated the Ludlovian of the Woolhope area with the old classification at Ludlow. Lower Elton Beds are recognizable in the base of the Lower Wootton Beds and the presence of *Monograptus* cf. *colonus* var. *compactus* and *M. varians* in the higher part of this division suggests a correlation with the Middle Elton Beds. Upper Elton Beds are proved by the abundance of *M. tumescens* in the Upper Wootton Beds. The predominance of shelly fossils, yet with sufficient diagnostic graptolites, in the Elton Beds of Woolhope assists in the correlation of Elton Beds at Usk and May Hill where graptolites are much rarer.

In northern Woolhope there is a complete succession of comparable thickness to that at Ludlow, but in the south of the area the series thins to 200 ft., the Upper Sleeves Oak Beds (i.e. Upper Bringewood Beds) being cut out altogether. A pebble bed occurs at the base of the Lower Bodenham Beds (i.e. Lower Leintwardine Beds) and a phosphatized fragment bed at the top of the Upper Bodenham Beds (Upper Leintwardine Beds).

(4) *Gorsley* (Column 8)

The quarries near Gorsley (Lawson, 1954) between Woolhope and May Hill, reveal that the Ludlovian rocks are reduced to a thickness of 11½ ft., comprising 7 ft. of

Lower Siltstones (i.e. Lower Leintwardine Beds) and $4\frac{1}{2}$ ft. of Upper Siltstones (i.e. Whitcliffe Beds). The new Tewkesbury to Ross motorway crosses this area and has exposed (SO 67152661) strata containing *Calymene neointermedia*, *Whitfieldella canalis* and *Sphaerirhynchia wilsoni*, together with phosphatized fragments and pebbles. This fauna suggests the presence of the very highest Lower Leintwardine Beds or the basal Upper Leintwardine Beds.

(5) *May Hill* (Column 9)

The Ludlovian Series at May Hill (Lawson, 1955) has a maximum thickness of 245 ft. Lower Elton Beds are represented by the similar Lower Flaxley Beds, although the occurrence in these latter of *Monograptus uncinatus* var. *orbatus* suggests that the Middle Elton Beds may be present in part. No Upper Elton Beds occur, even in their more shelly development as seen at Woolhope. A small thickness of Upper Bringewood Beds, although not in their Aymestry Limestone facies, can be recognized in the highest Upper Flaxley Beds at Blaisdon, where they contain *Favosites* and simple corals.

The base of the Upper Leintwardine Beds may be a foot or so above the base of the Lower Longhope Beds, which have been defined on the appearance of *Calymene neointermedia*, thereby incorporating strata with *Sphaerirhynchia wilsoni*. Since the paper on May Hill was written, *Chonetoides grayi* has been found in these Lower Longhope Beds (Upper Leintwardine Beds) at locality D in Text-fig. 2 of Lawson (1955 : 95). In some places a thin phosphatized fragment layer occurs at the base of these beds as well as at the top. The Upper Longhope Beds (Whitcliffe Beds) have not been subdivided.

(6) *Malvern*

The southern Malvern succession has been studied by Phipps (1957) but the results remain unpublished. The Elton Beds are non-graptolitic and show interesting lateral changes in their shelly fauna. The thicknesses of the Lower and Upper Bringewood Beds are complementary; the latter division comprises thick, massive limestone only in the west of the area. The Lower Leintwardine Beds develop conglomeratic layers towards the south-west (i.e. approaching the Gorsley Axis). One specimen of *Neobeyrichia lauensis* has been found in the Upper Leintwardine Beds. The Whitcliffe Beds have not been subdivided.

(7) *Newnham*

Near Aram's Farm, west of Newnham, a small inlier (SO 680109) of Ludlovian rocks appears between the Old Red Sandstone and the Triassic. Dr. H. C. Squirrell has recognized Elton or Lower Bringewood Beds, Lower Leintwardine Beds, Upper Leintwardine Beds and possibly Lower Whitcliffe Beds.

(8) *Tites Point*

At low tide Ludlovian rocks are exposed on the eastern shore of the River Severn (SO 692048). The oldest strata appear to be Lower Leintwardine Beds with layers of

limestone conglomerate ; the fauna includes solitary corals, large *Atrypa reticularis*, *Camarotoechia nucula*, *Protochonetes ludloviensis*, *Dayia navicula*, *Isorthis orbicularis*, *Sphaerirhynchia wilsoni* and small *Whitfieldella canalis*. No Upper Leintwardine Beds have been recognized. The Whitcliffe Beds appear to pass upwards conformably into reddish shaly siltstone with bands of mud pellets, specimens of *Lingula* and plants. These beds may represent a brackish water phase in late Ludlovian times for along the southern belt of the Silurian sea there seems to have been a tendency for brackish water or continental conditions to develop before the end of the Ludlovian (e.g. Cardiff, Llandovery and possibly Pembrokeshire and southern Ireland).

(9) *Central England*

The most complete and instructive section in the Ludlovian strata of this region is in the road section at Lye (SO 930845), described by King & Lewis (1912) but recently re-examined in order to compare it with the Ludlow succession. No Elton Beds or Lower Bringewood Beds are seen but the Upper Bringewood Beds are probably represented by the few feet of massive Sedgley Limestone still visible. The succeeding thinly bedded Sedgley Limestone (well exposed also at Beacon Hill, Sedgley, SO 919949) represents the Leintwardine Beds of the revised classification and is 35 ft. thick. The basal 8 ft. contain several calcareous pebble bands similar to those at the same stratigraphical level at May Hill, southern Woolhope, and the southern Malverns. At the top of the Sedgley Limestone Dr. E. V. Tucker has found a band of *Shaleria ornatella* which probably indicates the presence of the Upper Leintwardine Beds. A similar band was collected some years ago from a temporary excavation at Gornal (SO 919932). The Whitcliffe Beds at Lye are 25 ft. thick and yield the characteristic fauna. The Ludlow Bone Bed is here split into several thin layers over a thickness of 1 ft. and is succeeded by the Downton Castle Sandstone. The highest Whitcliffe Beds, the Ludlow Bone Bed and the basal shaly siltstones of the Downtonian are also well seen in the old railway cutting at Netherton (SO 936874).

(ii) *Basin Facies*

This section also includes the southern marginal areas of Llandovery and Pembrokeshire. For the Welsh Borderland and central Welsh areas a generalized succession was introduced in a paper describing a Geologists' Association excursion to the Ludlow district (Allender and others, 1959). Further details are given by Holland (1962) who also summarizes the differences in lithology and thickness between basin and shelf facies and discusses the correlation within the basin facies. The correlation with the shelf facies was also dealt with by Lawson and others (1956).

At Builth (column 11) and Cwm Craig Ddu (column 12) the Lower Ludlow Graptolitic Shales have been shown to include the zone of *Monograptus vulgaris* (Wood, 1900) but in other areas the beds below the *M. nilssoni*-*M. scanicus* Zone were not studied. The rich shelly fauna of the *Chonetoides grayi* Beds of Builth

BASIN FACIES

CLUN FOREST C

CRAIG DDU raw 1953	KNIGHTON Holland 1959	S.W. CLUN Earp 1940
tilestones	<i>Platyschisma helicites</i> Beds	<i>Platyschisma helica</i> Beds
<i>Dalmanella conica</i> Beds	Llan-Wen Hill Beds	<i>Dalmanella lunata</i> Beds
<i>Platyschisma striatella</i> Beds		
Transition Beds	Wern Quarry Beds	<i>Dayia navicula</i> Beds
	Knucklas	
<i>Platyschisma grayi</i> Beds	Castle Beds	
Upper <i>Angulula lata</i> Beds	uppermost Bailey Hill Beds	Main Contour Group
Lower <i>Angulula lata</i> Beds	Middle and Upper Bailey Hill Beds	
<i>Pterinea nuistriata</i> Beds		
<i>Graptolites</i> Ludstones	Lower Bailey Hill Beds	
Graptolitic Shales	Lower Ludlow Graptolitic Shales	Graptolitic L Ludlow Sh
12	13	14

• • • • Bone-Bed or Phosphatized

○ ○ ○ Conglomeratic bands

~~~~~ Erosion surface



- • • • Bone-Bed or Phosphatized Pebble-Bed
- ⊙ ⊙ ⊙ Conglomeratic bands
- ~~~~~ Erosion surface



provides a strong correlation link with the Upper Leintwardine Beds of Ludlow. The Clun Forest districts have been fully discussed by Holland (1959 : 470). Other areas for which revised successions have not yet been published are considered briefly below.

(1) *Brecon Anticlinal*

Kirk (1951) has so far published only a short summary of the succession in this extensive area. There is a general similarity to the Builth succession. The Striped Flags are the approximate equivalent of the Lower Ludlow Shelly Siltstones.

(2) *Bishop's Castle*

In the paper by Allender and others (1959) there is a brief survey of the Ludlovian rocks of this area. The succession is similar, especially in the upper part, to that at Knighton, but it is important to note that the *Neobeyrichia lauensis-Chonetoides grayi* assemblage occurs in strata equivalent in position to the Lower Knucklas Castle Beds of Knighton which lack this distinctive fauna. Also there are interesting local variations and facies changes at the base of the Lower Ludlow Shelly Siltstones and in the various graptolitic shales and shelly siltstones which lie below.

(3) *Radnor Forest*

Unpublished work by S. H. Straw and, more recently, by R. J. Bailey has shown that in the Radnor Forest area the Lower Ludlow Shelly Siltstones change laterally from the Clun Forest development, with its turbidite beds of calcareous siltstone, to the *Cyrtoceras* Mudstone facies of the Builth district.

(4) *Towy Anticline*

The Ludlovian rocks of the south-eastern flank of the Towy Anticline have been recently studied by both Price (1957) and Potter (1960). They have been able to correlate the succession with the revised classification at Ludlow. An important feature of the area is the development south-westwards of shallow water and even terrestrial deposits (e.g. the red Trichrûg Beds) in the Bringewoodian.

(5) *Pembrokeshire*

In west Pembrokeshire, the Grey Sandstone Series was assigned by the Geological Survey (Cantrill *et al.*, 1916 : 58) to the Ludlovian. Its base is difficult to define, and the junction with the overlying Red Marls is not necessarily a constant horizon. Fossils are scarce, particularly in the uppermost 800 ft. for which there is no positive evidence so far of Ludlovian age. Until current work on the Sandstone Series faunas is completed, no basis for correlation with the Welsh Borderland Ludlovian exists, and the assumption that the change of colour from grey to red marks the top of the Ludlovian is not necessarily valid (Walmsley 1962).



## VIII. LIST OF FOSSILS

Except where otherwise stated (under BRYOZOANS), this list includes only those fossils collected by the present writers.

Relative abundance is suggested by the following symbols :—

P = present

FC = fairly common

C = common

If it is considered that a particular fossil would be found at most of the exposures of a stratigraphical division with, say, half an hour's study, that fossil has been recorded as FC. A species recorded as P cannot be guaranteed to appear either at any given place or in any given time. A common fossil will normally be evident in the first five minutes, although it must be remembered that Ludlovian fossils tend to occur in bands.

|                                                              | Wenlock Shales | Wenlock Limestone | Lower Elton Beds | Middle Elton Beds | Upper Elton Beds | Lower Bringewood Beds | Upper Bringewood Beds | Lower Leintwardine Beds | Upper Leintwardine Beds | Lower Whitcliffe Beds | Upper Whitcliffe Beds |
|--------------------------------------------------------------|----------------|-------------------|------------------|-------------------|------------------|-----------------------|-----------------------|-------------------------|-------------------------|-----------------------|-----------------------|
| <b>ANTHOZOA</b>                                              |                |                   |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Entelophyllum articulatum</i> (Wahlenberg)                |                | P                 |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Favosites asper</i> d'Orbigny                             |                | P                 |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| — <i>gothlandicus</i> forma <i>forbesi</i> (Edwards & Haime) |                |                   |                  |                   |                  |                       | FC                    |                         |                         |                       |                       |
| <i>Favosites</i> spp.                                        |                | FC                |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Halysites catenularius</i> (Linnaeus)                     |                |                   | P                |                   |                  |                       | P                     |                         |                         |                       |                       |
| <i>Heliolites interstinctus</i> (Linnaeus)                   |                | FC                |                  |                   |                  |                       | FC                    |                         |                         |                       |                       |
| <i>Rhabdocyclus porpitoides</i> (Lang & Smith)               |                |                   |                  |                   |                  | P                     | P                     |                         |                         |                       |                       |
| <i>Thecia grayana</i> Edwards & Haime                        |                | P                 | P                |                   |                  |                       | FC                    |                         |                         |                       |                       |
| solitary corals <sup>1</sup>                                 | P              | P                 | P                |                   |                  | P                     | FC                    | P                       |                         |                       |                       |
| <b>STROMATOPOROIDEA</b>                                      |                |                   |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Stromatopora carteri</i> Nicholson                        |                | P                 |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| — sp.                                                        |                |                   |                  |                   |                  |                       | P                     |                         |                         |                       |                       |
| <b>BRYOZOANS<sup>2</sup></b>                                 |                |                   |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Batostoma</i> sp.                                         |                |                   |                  |                   |                  | P                     | C                     | FC                      |                         |                       |                       |
| <i>Batostomella hemiseptensis</i> Owen                       |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Batostomella hexamesopora</i> Owen                        | P              |                   |                  |                   |                  | C                     | P                     | P                       |                         |                       |                       |
| <i>Bythopora parallela</i> Owen                              | P              |                   |                  |                   |                  | FC                    | FC                    |                         |                         |                       |                       |



BRYOZOANS<sup>2</sup>—contd.

|                                                                                    | Wenlock Shales | Wenlock Limestone | Lower Elton Beds | Middle Elton Beds | Upper Elton Beds | Lower Bringewood Beds | Upper Bringewood Beds | Lower Leintwardine Beds | Upper Leintwardine Beds | Lower Whitcliffe Beds | Upper Whitcliffe Beds |
|------------------------------------------------------------------------------------|----------------|-------------------|------------------|-------------------|------------------|-----------------------|-----------------------|-------------------------|-------------------------|-----------------------|-----------------------|
| <i>Calamotrypa millichopensis</i> Owen . . . . .                                   |                |                   |                  |                   |                  | FC                    | FC                    |                         |                         |                       |                       |
| <i>Dekayella megacanthopora</i> Owen . . . . .                                     |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Dekayella ramosa</i> Owen . . . . .                                             |                |                   |                  |                   |                  | P                     | P                     | P                       |                         |                       |                       |
| <i>Dekayella whitcliffensis</i> Owen . . . . .                                     |                |                   |                  |                   |                  |                       |                       |                         |                         |                       | C                     |
| <i>Eridotrypa umbonensis</i> Owen . . . . .                                        |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Favositella interpuncta</i> (Quenstedt) . . . . .                               |                |                   |                  |                   | P                | P                     | P                     |                         |                         |                       |                       |
| <i>Fistulipora crassa</i> Lonsdale . . . . .                                       |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Fistulipora strawi</i> Owen . . . . .                                           |                |                   | P                |                   | FC               | C                     | C                     | C                       |                         |                       |                       |
| <i>Fistulipora umbrosa</i> Owen . . . . .                                          |                |                   |                  |                   |                  | P                     | FC                    |                         |                         |                       |                       |
| <i>Leioclema explanatum</i> Bassler . . . . .                                      |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Leioclema ludlovensis</i> Owen . . . . .                                        |                |                   |                  |                   |                  | C                     | C                     | P                       |                         | P                     | P                     |
| <i>Leptotrypella leintwardinensis</i> Owen . . . . .                               |                |                   |                  |                   |                  |                       |                       | P                       |                         |                       |                       |
| <i>Monotrypa crenulata</i> Nicholson . . . . .                                     |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Monotrypa fiabellata</i> Owen . . . . .                                         |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Monotrypa patera</i> Owen . . . . .                                             |                |                   |                  |                   |                  | C                     | FC                    |                         |                         |                       |                       |
| <i>Nematopora hexagona</i> Owen . . . . .                                          |                |                   | FC               |                   | FC               | C                     |                       |                         |                         |                       |                       |
| <i>Orbignyella fibrosa</i> (Lonsdale) . . . . .                                    |                |                   |                  |                   |                  |                       |                       | C                       |                         | P                     |                       |
| <i>Ptilodictya gracile</i> Owen . . . . .                                          |                |                   | P                |                   |                  | FC                    | C                     |                         |                         |                       |                       |
| <i>Ptilodictya lanceolata</i> (Goldfuss) . . . . .                                 |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Rhombopora minima</i> Owen . . . . .                                            |                |                   | FC               |                   | FC               | C                     | C                     |                         |                         |                       |                       |
| <i>Rhombopora mesopora</i> Owen . . . . .                                          |                |                   |                  |                   |                  |                       |                       |                         | FC                      |                       |                       |
| undetermined bryozoans . . . . .                                                   | P              | P                 |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| BRACHIOPODA                                                                        |                |                   |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Atrypa reticularis</i> (Linnaeus) . . . . .                                     |                | FC                | FC               | P                 |                  | C                     | C                     | C                       | P-C <sup>3</sup>        |                       |                       |
| <i>Brachyprion</i> sp. nov. . . . .                                                | P              |                   |                  |                   | P                | FC                    | P                     |                         |                         |                       |                       |
| <i>Camarotoechia nucula</i> (J. de C. Sowerby) . . . . .                           |                | P                 |                  | P                 | P                | P                     | P                     | C                       | C                       | C                     | C                     |
| <i>Chonetes lepisma</i> (J. de C. Sowerby) . . . . .                               |                |                   |                  |                   | FC <sup>4</sup>  | FC                    | P                     | FC                      | P                       |                       |                       |
| — <i>minimus</i> (J. de C. Sowerby) . . . . .                                      |                |                   | P                |                   |                  | P                     |                       |                         |                         |                       |                       |
| <i>Chonetoidea grayi</i> (Davidson) . . . . .                                      | P              |                   | FC               | FC                | P                | P                     |                       | P                       | FC <sup>5</sup>         |                       |                       |
| <i>Conchidium knighti</i> (J. Sowerby) . . . . .                                   |                |                   |                  |                   |                  |                       | C                     |                         |                         |                       |                       |
| <i>Craniops</i> [ <i>Pholidops</i> ] <i>implicata</i> (J. de C. Sowerby) . . . . . |                |                   |                  |                   |                  | P                     | P                     | P                       | P                       |                       | P                     |
| <i>Cyrtia exporrecta</i> (Wahlenberg) . . . . .                                    | P              |                   |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| " <i>Dalmanella</i> " spp. . . . .                                                 |                |                   |                  |                   |                  | P                     | P                     |                         | P                       |                       |                       |
| <i>Dayia navicula</i> (J. de C. Sowerby) . . . . .                                 |                |                   |                  | P                 |                  | P                     | P                     | C                       | FC                      | FC <sup>6</sup>       |                       |
| <i>Dicoelosia</i> [ <i>Bilobites</i> ] <i>biloba</i> (Linnaeus) . . . . .          | P              |                   | P                |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Dolerorthis rustica</i> (J. de C. Sowerby) . . . . .                            | P              | P                 | P                |                   |                  |                       |                       |                         |                         |                       |                       |
| <i>Eospirifer plicatellus</i> (Linnaeus) . . . . .                                 |                |                   |                  |                   |                  |                       |                       |                         |                         |                       |                       |
| — <i>radiatus</i> (J. de C. Sowerby) . . . . .                                     |                | P                 |                  | P                 |                  |                       | P                     |                         |                         |                       |                       |
| <i>Fardenia pecten</i> (Linnaeus) <sup>7</sup> . . . . .                           |                |                   |                  |                   |                  | P                     |                       |                         |                         |                       |                       |







LAMELLIBRANCHIA—*contd.*

*Modiolopsis complanata* (J. de C. Sowerby)

*Nuculites* spp.

*Plethomytilus* [Mytilus] *mytilimeris*  
(Conrad)

|                             |   |   |   |
|-----------------------------|---|---|---|
| <i>Pterinea nupera</i> Reed | . | . | . |
| — spp.                      | . | . | . |

*Pteronitella retroflexa* (Wahlenberg) .

*Slava* [*Cardiola*] *interrupta* (Sowerby)

*Tolmaia* [*Pterinea*] *sowerbyi* (McCoy)

## GASTROPODA

*Bellerophon* sp. . . . .

*Bembexia* [*Murchisonia*] *lloydi* (J. de.  
C. Sowerby)

*Bucanopsis* [*Bellerophon*] *expansus*  
(J. de C. Sowerby)

*Cyclonema* [Turbo] *corallii* (J. de C. Sowerby)

*Hormotoma* [*Murchisonia*] *articulata*  
(J. de C. Sowerby)

*Liospira* [*Pleurotomaria*] *striatissima*  
(Salter)

*Loxonema* [*Holopella*] sp.<sup>15</sup>

*Murchisonia* sp. . . . .

*Poleumita* [*Horiostoma*] *globosa*  
(Schlotheim) . . . . .

— [—] *discors* (J. de C. Sowerby)

## CEPHALOPODA

*Cyrtoceras* sp. . . . .

*Dawsonoceras annulatum* (J. Sowerby)

*Kionoceras angulatum* (Wahlenberg) .

*Lituities ibex* J. de C. Sowerby . . . . .

*Michelinoceras* [*Orthoceras*] cf. *argus*  
(Barrande)

— [—] *bullatum* (J. de C. Sowerby)

— [—] cf. *gregarium* (J. de C. Sowerby)

— [—] *ibex* (J. de C. Sowerby) .

— [—] *imbricatum* (Wahlenberg)

[illegible]







[illegible]

## NOTES

1. These are small trochoid corals, many of which resemble *Phaulactis*.
2. Dr. D. E. Owen has kindly supplied the list of Ludlovian Bryozoans from the Ludlow District. Details of his work are contained in Owen (1962).
3. Commoner in the east of the area.
4. Fairly common locally.
5. Fairly common in bands.
6. Fairly common in the basal beds.
7. According to Boucot (1959) the genus *Fardenia* is restricted to the upper Ordovician and Lower Llandovery. The species *Fardenia pecten* (Linnaeus) is assigned to the new genus *Chilidiopsis* Boucot.
8. Very common in bands in the topmost beds.
9. Professor Boucot (1960) assigns the familiar Ludlovian species *Dalmanella orbicularis* (J. de C. Sowerby) to the genus *Isorthis* Kozłowski and erects the new genus *Salopina* for the species *Dalmanella* [*Orthis*] *lunata* (J. de C. Sowerby).
10. Commoner in the west of the area.
11. See Muir-Wood (1962).
12. Commoner in the east of the area, particularly in the higher beds.
13. Less common in the west of the area.
14. A more correct designation is probably *Amphistrophia funiculata*. See Williams (1953: Plate 12).
15. According to Knight & others (1960: 1311) *Holopella* M'Coy is a synonym of *Loxonema* Phillips.
16. According to Howell (1962: W163) *Serpulites longissimus* J. de C. Sowerby is the type species of the genus *Campylites* Eichwald, 1856.
17. Fairly common in bands.
18. See Dean (1960).



19. According to Tripp (1962) the *Encrinurus punctatus* group is represented in Britain by *E. tuberculatus* (Buckland) in the Wenlockian and *E. stubblefieldi* Tripp in the Ludlovian.
20. Fairly common in bands.
21. See Martinsson (1962).
22. Fairly common in bands, especially in the west.
23. According to Kjellesvig-Waering (1961) four species are present in the "Upper Ludlow" of the Ludlow District. Three of these are from the Whitcliffe at Ludlow but no more precise stratigraphical information is available. None is recorded from lower in the Silurian succession of the district but many Downtonian forms (here included within the Silurian) are described.
24. Fairly common in the basal beds; mostly round but some pentagonal.
25. Present in the topmost beds only.

#### IX. ACKNOWLEDGMENTS

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## APPENDIX 1 : LIST OF LOCALITIES

In the following list numbers 1 to 77 refer to localities given in the detailed descriptions of important areas (Section IV) and their positions are shown in Text-fig. 7 (Whitcliffe: localities 1-13), Text-fig. 8 (Wigmore Road: localities 14-28), Text-fig. 9 (Mary Knoll Valley: localities 29-37) and Text-fig. 10 (Downton Gorge and Burrington: localities 38-77). The remainder of the list is arranged according to National Grid squares, starting in the south-west. Standard localities (Sections III and VI) and selected localities for the stratigraphical divisions (Section III) (where not included under localities 1-77) are to be found in this part of the list. They are indicated throughout the complete list by the letters "S" (standard locality) and "R" (selected locality representative of a stratigraphical division) in the final column. The National Grid letters in all cases are SO. Abbreviations for the stratigraphical divisions exposed at the localities are as listed on p. 103. In most cases the location of each exposure is also given as an approximate bearing and distance from a point indicated by name on the 1:25000 Ordnance Survey sheets SO47 and SO57.

| Locality number   | Grid reference | Stratigraphical divisions exposed | Location                                                                                                   | "S" and "R" localities |
|-------------------|----------------|-----------------------------------|------------------------------------------------------------------------------------------------------------|------------------------|
| <i>Whitcliffe</i> |                |                                   |                                                                                                            |                        |
| 1                 | 50747428       | L.L.B.                            | small exposure below path 180 yds S.S.E. Dinham Bridge                                                     |                        |
| 2                 | 50717429       | L.L.B.                            | exposure behind seat 160 yds S.S.E. Dinham Bridge                                                          |                        |
| 3                 | 50717428       | L.W.B.<br>U.L.B.<br>L.L.B.        | cliff 180 yds S.S.E. Dinham Bridge (standard sections for both L.L.B./U.L.B. and U.L.B./L.W.B. boundaries) | S                      |
| 4                 | 50827421       | U.L.B.                            | pathside exposure 290 yds S.E. Dinham Bridge                                                               |                        |
| 5                 | 50907417       | L.W.B.                            | pathside exposure 380 yds W. Ludford Bridge                                                                |                        |
| 6                 | 50967414       | U.W.B.<br>L.W.B.                  | Whitcliffe quarry 345 yds W.S.W. Ludford Bridge                                                            | S                      |
| 7                 | 51237413       | D.C.S.<br>B.B.<br>U.W.B.          | exposure at junction of "Ludford Lane" and Leominster road 80 yds S.S.W. Ludford Bridge                    | S                      |
| 8                 | 50717425       | L.W.B.                            | path exposure 210 yds S. Dinham Bridge                                                                     | R                      |
| 9                 | 50657433       | L.W.B.                            | pathside exposure 120 yds S.S.W. Dinham Bridge                                                             |                        |
| 10                | 50657434       | U.L.B.                            | small pathside exposure 110 yds S.S.W. Dinham Bridge                                                       |                        |
| 11                | 50627440       | U.L.B.<br>L.L.B.                  | path section 70 yds S.W. Dinham Bridge                                                                     | R                      |
| 12                | 50627442       | L.W.B.                            | exposures 70 yds W.S.W. Dinham Bridge                                                                      |                        |
| 13                | 50627445       | L.W.B.                            | small quarry 70 yds W. Dinham Bridge                                                                       |                        |



| Locality number          | Grid reference | Stratigraphical divisions exposed | Location                                                        | "S" and "R" localities |
|--------------------------|----------------|-----------------------------------|-----------------------------------------------------------------|------------------------|
| <i>Wigmore Road</i>      |                |                                   |                                                                 |                        |
| 14                       | 47167301       | W.L.                              | roadside quarry 460 yds E.S.E. Monstay                          | R                      |
| 15                       | 47227304       | W.L.                              | roadside quarry 520 yds E.S.E. Monstay                          |                        |
| 16                       | 47267301       | L.E.B.                            | quarry in coppice 600 yds E.S.E. Monstay                        | SR                     |
|                          |                | W.L.                              |                                                                 |                        |
| 17                       | 47777324       | M.E.B.                            | stream exposure 450 yds S.S.W. Gorsty                           | R                      |
| 18                       | 47897357       | U.E.B.                            | roadside exposure 70 yds S.S.W. Gorsty                          | R                      |
| 19                       | 48287377       | L.B.B.                            | roadside exposure 170 yds N.N.E. Mary Knoll House               | R                      |
| 20                       | 48557369       | U.B.B.                            | trackside quarry 400 yds E. Mary Knoll House                    | R                      |
| 21                       | 48577360       | —                                 | viewpoint at summit of Mary Knoll                               |                        |
| 22                       | 47327382       | U.B.B.                            | landslip exposure 700 yds W.N.W. Gorsty                         | R                      |
| 23                       | 48747389       | U.B.B.                            | roadside exposure 660 yds E.N.E. Mary Knoll House               | R                      |
| 24                       | 48887392       | L.L.B.                            | roadside quarry 810 yds E.N.E. Mary Knoll House                 | R                      |
| 25                       | 49107399       | L.L.B.                            | roadside quarry 1080 yds E.N.E. Mary Knoll House                | R                      |
| 26                       | 49227407       | U.L.B.                            | roadside exposure 1230 yds E.N.E. Mary Knoll House              | R                      |
| 27                       | 49307412       | U.L.B.                            | roadside exposure 840 yds W. Whitcliffe North                   | R                      |
| 28                       | 49797430       | L.W.B.                            | roadside exposure 330 yds N.W. Whitcliffe North                 | R                      |
| <i>Mary Knoll Valley</i> |                |                                   |                                                                 |                        |
| 29                       | 49737244       | L.W.B.                            | large quarry 270 yds E.S.E. Sunnyhill Cottages                  | R                      |
| 30                       | 49537255       | L.L.B.                            | large quarry near Sunnyhill Cottages (Sunnyhill Quarry)         | S                      |
|                          |                | U.B.B.                            |                                                                 |                        |
| 31                       | 49437255       | U.B.B.                            | small quarry 100 yds N.W. Sunnyhill Cottages                    |                        |
| 32                       | 49367260       | L.B.B.                            | track exposure 180 yds N.W. Sunnyhill Cottages                  |                        |
| 33                       | 49347263       | L.B.B.                            | roadside section 240 yds N.W. Sunnyhill Cottages                | R                      |
| 34                       | 49307268       | L.B.B.                            | roadside section 290 yds N.W. Sunnyhill Cottages                |                        |
| 35                       | 49337268       | U.B.B.                            | small quarry 270 yds N.W. Sunnyhill Cottages                    | R                      |
| 36                       | 49437270       | L.L.B.                            | crag 210 yds N.N.W. Sunnyhill Cottages                          |                        |
| 37                       | 49427242       | U.L.B.                            | exposure in overgrown track 130 yds S.S.W. Sunnyhill Cottages   |                        |
| <i>Downton Gorge</i>     |                |                                   |                                                                 |                        |
| 38                       | 43657220       | W.S.                              | exposures in wooded bank 180 yds N.N.E. Burrington Bridge       | R                      |
| 39                       | 43507228       | W.S.                              | exposures in wooded bank 280 yds N.N.W. Burrington Bridge       |                        |
| 40                       | 43347227       | W.S.                              | trackside exposure 370 yds N.W. Burrington Bridge               | R                      |
| 41                       | 43277232       | W.L.                              | small exposure above wooded bank 470 yds N.W. Burrington Bridge |                        |
| 42                       | 43237273       | M.E.B.                            | exposure above path 90 yds N.N.W. Owney Cottage                 |                        |
| 43                       | 43037280       | U.E.B.                            | exposures in steep wooded slope 380 yds S. Bow Bridge           | R                      |
| 44                       | 42897296       | L.B.B.                            | small quarry 60 yds N. of eastern end Downton Bridge            | R                      |
| 45                       | 43067313       | U.B.B.                            | riverside exposures just S. Bow Bridge                          | R                      |
| 46                       | 43117320       | L.L.B.                            | small exposure below tree 100 yds N.E. Bow Bridge               |                        |
| 47                       | 43197316       | U.L.B.                            | very small trackside exposures 150 yds E.N.E. Bow Bridge        |                        |



| Locality number   | Grid reference | Stratigraphical divisions exposed | Location                                                          | "S" and "R" localities |
|-------------------|----------------|-----------------------------------|-------------------------------------------------------------------|------------------------|
| 48                | 43297312       | U.L.B.                            | quarry 260 yds E. Bow Bridge                                      |                        |
| 49                | 43457352       | L.W.B.                            | quarry at western side Hay Mill                                   | R                      |
| 50                | 43777358       | L.W.B.                            | riverside exposures E. Hay Mill                                   | R                      |
| 51                | 43987400       | L.W.B.                            | river cliff 630 yds S.W. Castle Bridge                            |                        |
| 52                | 44027390       | U.W.B.                            | quarried crags above river 670 yds S.W. Castle Bridge             | R                      |
| 53                | 44107367       | U.W.B.<br>L.W.B.                  | quarries 820 yds S.S.W. Castle Bridge                             | R                      |
| 54                | 44167411       | U.W.B.                            | exposures above riverside path 400 yds S.W. Castle Bridge         | R                      |
| 55                | 44277415       | U.W.B.                            | exposures above riverside path 260 yds S.W. Castle Bridge         |                        |
| 56                | 44427425       | U.W.B.                            | pathside section 70 yds S.W. Castle Bridge                        | R                      |
| 57                | 44497427       | D.C.S.<br>B.B.                    | trackside quarry near S. end Castle Bridge                        | R                      |
| 58                | 44427402       | D.C.S.<br>U.W.B.                  | track section 320 yds S.S.W. Castle Bridge                        |                        |
| 59                | 44497409       | T.S.<br>D.C.S.                    | track section 230 yds S. Castle Bridge                            |                        |
| <i>Burrington</i> |                |                                   |                                                                   |                        |
| 60                | 44387242       | W.S.                              | laneside section 400 yds N.N.E. Burrington Church                 |                        |
| 61                | 44337250       | W.S.                              | laneside section 460 yds N.N.E. Burrington Church                 | R                      |
| 62                | 44257253       | W.L.<br>W.S.                      | lane section 490 yds N. Burrington Church                         |                        |
| 63                | 44257255       | W.L.                              | quarry E. of lane 510 yds N. Burrington Church                    | R                      |
| 64                | 44177257       | W.L.                              | lane section 540 yds N.N.W. Burrington Church                     |                        |
| 65                | 44377266       | W.L.                              | quarry south of lane 650 yds N.N.E. Burrington Church             | R                      |
| 66                | 44507277       | L.E.B.                            | small laneside exposure 800 yds N.N.E. Burrington Church          |                        |
| 67                | 44537278       | L.E.B.                            | small stream exposure N. of lane 840 yds N.N.E. Burrington Church |                        |
| 68                | 44147263       | W.L.                              | track section 620 yds N.N.W. Burrington Church                    |                        |
| 69                | 43897278       | M.E.B.<br>L.E.B.                  | stream section 710 yds E.N.E. Owney Cottage                       | SR                     |
| 70                | 43667266       | L.E.B.                            | stream section 450 yds E. Owney Cottage                           | R                      |
| 71                | 43617265       | L.E.B.                            | stream section 380 yds E. Owney Cottage                           |                        |
| 72                | 43527264       | M.E.B.                            | stream section 290 yds E. Owney Cottage                           | R                      |
| 73                | 43487262       | L.E.B.                            | stream section 250 yds E.S.E. Owney Cottage                       | R                      |
| 74                | 43387264       | M.E.B.                            | stream section 170 yds E. Owney Cottage                           |                        |
| 75                | 43377263       | M.E.B.                            | stream section 120 yds E.S.E. Owney Cottage                       | R                      |
| 76                | 43677283       | U.E.B.<br>M.E.B.                  | trackside section 920 yds E. Downton Bridge                       | S                      |
| 77                | 43757307       | L.L.B.<br>U.B.B.                  | scarp top quarry 790 yds E. Bow Bridge                            | R                      |



| Locality number                                               | Grid reference | Stratigraphical divisions exposed | Location                                                           | "S" and "R" localities |
|---------------------------------------------------------------|----------------|-----------------------------------|--------------------------------------------------------------------|------------------------|
| <i>Other localities arranged under Kilometre Grid Squares</i> |                |                                   |                                                                    |                        |
| <i>Grid Square 43/71</i>                                      |                |                                   |                                                                    |                        |
| 78                                                            | 43057142       | W.S.                              | small exposure in wooded bank 180 yds W. The Willows               |                        |
| 79                                                            | 43237172       | W.S.                              | small riverside exposures 550 yds S.W. Burrington Bridge           |                        |
| 80                                                            | 43457187       | W.S.                              | riverside exposure 270 yds S.W. Burrington Bridge                  |                        |
| <i>Grid Square 43/72</i>                                      |                |                                   |                                                                    |                        |
| 81                                                            | 43097283       | L.B.B.                            | uppermost exposures on wooded slope 350 yds S.S.E. Bow Bridge      |                        |
| 82                                                            | 43257264       | M.E.B.                            | stream exposure 20 yds S.W. Owey Cottage                           |                        |
| 83                                                            | 43337294       | U.B.B.                            | small exposures 390 yds S.E. Bow Bridge                            |                        |
| 84                                                            | 43957261       | W.L.                              | trackside exposures 660 yds N.N.W. Burrington Church               |                        |
| <i>Grid Square 43/73</i>                                      |                |                                   |                                                                    |                        |
| 85                                                            | 43417322       | L.W.B.                            | exposure 410 yds E.N.E. Bow Bridge                                 |                        |
| 86                                                            | 43437331       | L.W.B.                            | quarry 260 yds S.S.W. Hay Mill                                     |                        |
| 87                                                            | 43567333       | L.W.B.                            | quarry 240 yds S.S.E. Hay Mill                                     |                        |
| 88                                                            | 43677340       | L.W.B.                            | track section 260 yds S.E. Hay Mill                                |                        |
| 89                                                            | 43957358       | L.W.B.                            | quarry 530 yds E. Hay Mill                                         |                        |
| <i>Grid Square 44/71</i>                                      |                |                                   |                                                                    |                        |
| 90                                                            | 44147198       | W.S.                              | roadside exposures 160 yds S.E. Burrington Church                  |                        |
| 91                                                            | 44247190       | W.S.                              | exposures in sides of sunken lanes 230 yds S. Burrington Church    |                        |
| 92                                                            | 44877180       | W.S.                              | small exposures on Bowburnet Hill 790 yds E.S.E. Burrington Church |                        |
| <i>Grid Square 44/72</i>                                      |                |                                   |                                                                    |                        |
| 93                                                            | 44227275       | W.L.                              | stream section 740 yds N. Burrington Church                        |                        |
| 94                                                            | 44427286       | M.E.B.                            | stream section 970 yds W.S.W. New House                            |                        |
| 95                                                            | 44517285       | M.E.B.                            | small ditch exposure 880 yds W.S.W. New House                      |                        |
| 96                                                            | 44557287       | M.E.B.                            | small stream exposure 830 yds W.S.W. New House                     |                        |
| 97                                                            | 44577288       | M.E.B.                            | stream section 800 yds W.S.W. New House                            |                        |
| 98                                                            | 44627285       | L.E.B.                            | stream section 750 yds W.S.W. New House                            |                        |
| 99                                                            | 44667239       | W.S.                              | small exposure 590 yds N.E. Burrington Church                      |                        |
| 100                                                           | 44787240       | W.S.                              | track sections 700 yds N.E. Burrington Church                      | R                      |
| 101                                                           | 44787280       | L.E.B.                            | laneside (stream) section 600 yds W.S.W. New House                 | R                      |
| 102                                                           | 44917281       | W.L.                              | trackside exposure 450 yds W.S.W. New House                        |                        |
| 103                                                           | 44937247       | W.L.                              | track section 700 yds S.S.W. New House                             |                        |
| <i>Grid Square 44/73</i>                                      |                |                                   |                                                                    |                        |
| 104                                                           | 44067308       | L.B.B.                            | small exposure 830 yds S.E. Hay Mill                               |                        |
| 105                                                           | 44127323       | L.L.B.<br>U.B.B.                  | scarp top quarry 790 yds E.S.E. Hay Mill                           |                        |



| Locality number          | Grid reference | Stratigraphical divisions exposed | Location                                                   | "S" and "R" localities |
|--------------------------|----------------|-----------------------------------|------------------------------------------------------------|------------------------|
| 106                      | 44187358       | L.W.B.                            | quarry 870 yds S.S.W. Castle Bridge                        |                        |
| 107                      | 44427307       | U.E.B.                            | small exposure 970 yds W.N.W. New House                    | R                      |
| 108                      | 44977388       | U.W.B.                            | head of small stream 730 yds S.E. Castle Bridge            |                        |
| <i>Grid Square 45/72</i> |                |                                   |                                                            |                        |
| 109                      | 45017285       | W.L.                              | track section 330 yds W.S.W. New House                     |                        |
| 110                      | 45127276       | W.L.                              | stream section 300 yds S.W. New House                      |                        |
| 111                      | 45127288       | W.L.                              | trackside exposures 200 yds S.W. New House                 |                        |
| 112                      | 45297273       | W.L.                              | stream section 280 yds S. New House                        |                        |
| 113                      | 45377275       | W.L.                              | stream section 280 yds S.S.E. New House                    |                        |
| 114                      | 45587238       | W.S.                              | track section 760 yds S.S.E. New House                     | R                      |
| 115                      | 45647207       | W.S.                              | stream exposures 610 yds W.N.W. Aston Church               |                        |
| 116                      | 45827253       | W.L.                              | trackside exposures 800 yds S.E. New House                 |                        |
| 117                      | 45877281       | W.L.                              | stream exposure 690 yds E.S.E. New House                   |                        |
| 118                      | 45957263       | W.L.                              | trackside section at west end Monstay Rough                |                        |
| <i>Grid Square 45/73</i> |                |                                   |                                                            |                        |
| 119                      | 45267302       | M.E.B.                            | small exposure just W. New House                           |                        |
| 120                      | 45377358       | U.L.B.                            | trackside exposure 680 yds N.N.E. New House                |                        |
| 121                      | 45407369       | U.L.B.                            | small quarry above track 810 yds N.N.E. New House          | R                      |
| 122                      | 45417353       | L.L.B.                            | trackside exposure 1070 yds S.W. Deepwood                  |                        |
| 123                      | 45467353       | L.L.B.                            | trackside exposure 660 yds N.N.E. New House                |                        |
| 124                      | 45467385       | U.W.B.                            | stream section 800 yds S.W. Deepwood                       |                        |
|                          |                | L.W.B.                            |                                                            |                        |
| 125                      | 45507368       | U.L.B.                            | trackside exposure 840 yds N.N.E. New House                | R                      |
| 126                      | 45657348       | L.L.B.                            | trackside exposure 1000 yds S.S.W. Deepwood                |                        |
| 127                      | 45807353       | U.B.B.                            | joint surfaces exposed by landslip 870 yds S.S.W. Deepwood | R                      |
| 128                      | 45827344       | U.B.B.                            | trackside exposure 950 yds S.S.W. Deepwood                 |                        |
| 129                      | 45877375       | L.W.B.                            | trackside section 630 yds S.S.W. Deepwood                  | R                      |
|                          |                | U.L.B.                            |                                                            |                        |
|                          |                | L.L.B.                            |                                                            |                        |
| 130                      | 45907363       | L.L.B.                            | trackside exposure 740 yds S.S.W. Deepwood                 |                        |
| 131                      | 45957352       | U.B.B.                            | stream section 850 yds S. Deepwood                         | S                      |
|                          |                | L.B.B.                            |                                                            |                        |
| 132                      | 45957376       | L.L.B.                            | small excavation west of track 590 yds S.S.W. Deepwood     |                        |
| 133                      | 45977370       | L.L.B.                            | trackside exposure 650 yds S.S.W. Deepwood                 |                        |
| 134                      | 45977380       | L.L.B.                            | quarry 540 yds S.S.W. Deepwood                             |                        |
| <i>Grid Square 45/74</i> |                |                                   |                                                            |                        |
| 135                      | 45527405       | D.C.S.                            | trackside exposure 600 yds W.S.W. Deepwood                 |                        |
| 136                      | 45577403       | Downton Bone Bed                  | trackside exposure 600 yds W.S.W. Deepwood                 |                        |
| 137                      | 45757406       | B.B. U.W.B.                       | small quarry south of track 400 yds S.W. Deepwood          | R                      |



| Locality number          | Grid reference | Stratigraphical divisions exposed   | Location                                          | "S" and "R" localities |
|--------------------------|----------------|-------------------------------------|---------------------------------------------------|------------------------|
| 138                      | 45877400       | W.B.                                | quarry near track 350 yds S.S.W. Deepwood         |                        |
| 139                      | 45997407       | T.S.<br>D.C.S.<br>(fault)<br>U.W.B. | stream section north of track 230 yds S. Deepwood |                        |
| <i>Grid Square 46/71</i> |                |                                     |                                                   |                        |
| 140                      | 46977196       | W.L.                                | small quarry 280 yds E. Juniper Cottage           | R                      |
| <i>Grid Square 46/72</i> |                |                                     |                                                   |                        |
| 141                      | 46257216       | W.S.                                | stream section 400 yds N.N.E. Aston Church        | R                      |
| 142                      | 46537204       | W.S.                                | stream exposure 500 yds E.N.E. Aston Church       |                        |
| 143                      | 46837280       | W.L.                                | small quarry (hen-run) on N. side Wigmore Road    |                        |
| <i>Grid Square 46/73</i> |                |                                     |                                                   |                        |
| 144                      | 46027368       | U.B.B.                              | trackside exposures 660 yds S. Deepwood           |                        |
| 145                      | 46027377       | L.L.B.                              | exposure 570 yds S. Deepwood                      |                        |
| 146                      | 46027387       | U.L.B.                              | trackside exposure 460 yds S. Deepwood            |                        |
| 147                      | 46037391       | L.W.B.                              | trackside exposure 410 yds S. Deepwood            |                        |
| 148                      | 46117319       | U.E.B.                              | trackside exposure 730 yds W. Monstay             |                        |
| 149                      | 46117361       | L.B.B.                              | exposure 740 yds S. Deepwood                      |                        |
| 150                      | 46177354       | L.B.B.                              | exposure 830 yds S.S.E. Deepwood                  |                        |
| 151                      | 46197363       | L.L.B.                              | exposure 740 yds S.S.E. Deepwood                  |                        |
| 152                      | 46217357       | U.B.B.                              | exposure 800 yds S.S.E. Deepwood                  |                        |
| 153                      | 46327327       | U.E.B.                              | trackside exposure 520 yds W.N.W. Monstay         |                        |
| 154                      | 46417398       | L.L.B.                              | exposure 540 yds S.E. Deepwood                    |                        |
| 155                      | 46737393       | W.B.                                | trackside exposure 850 yds S.E. Deepwood          |                        |
| 156                      | 46967373       | U.B.B.                              | trackside exposure 1050 yds W.N.W. Gorsty         |                        |
| 157                      | 46987328       | M.E.B.                              | trackside exposure 1100 yds W.S.W. Gorsty         |                        |
| 158                      | 46997336       | U.E.B.                              | trackside exposure 1070 yds W.S.W. Gorsty         |                        |
| <i>Grid Square 46/74</i> |                |                                     |                                                   |                        |
| 159                      | 46137425       | R.D.<br>T.S.                        | stream section 100 yds E. Deepwood                |                        |
| <i>Grid Square 47/71</i> |                |                                     |                                                   |                        |
| 160                      | 47207189       | W.L.                                | trackside exposure 500 yds E.S.E. Juniper Cottage |                        |
| 161                      | 47257187       | W.L.                                | trackside exposure 600 yds E.S.E. Juniper Cottage |                        |
| 162                      | 47267184       | L.E.B.<br>W.L.                      | trackside exposure 600 yds E.S.E. Juniper Cottage | R                      |
| 163                      | 47267190       | W.L.                                | trackside exposure 600 yds E.S.E. Juniper Cottage | R                      |
| 164                      | 47587158       | U.E.B.                              | trackside exposure 950 yds S.S.W. High Vinnals    | R                      |
| 165                      | 47607165       | U.E.B.                              | small quarry 870 yds S.S.W. High Vinnals          | R                      |
| 166                      | 47657170       | U.E.B.                              | small quarry 800 yds S.S.W. High Vinnals          |                        |
| <i>Grid Square 47/72</i> |                |                                     |                                                   |                        |
| 167                      | 47027297       | W.L.                                | trackside exposure 180 yds N.N.E. Juniper Cottage |                        |
| 168                      | 47127292       | W.L.                                | quarry in wood at Pitch Coppice                   |                        |



| Locality number          | Grid reference | Stratigraphical divisions exposed | Location                                           | "S" and "R" localities |
|--------------------------|----------------|-----------------------------------|----------------------------------------------------|------------------------|
| 169                      | 47207277       | W.L.                              | small trackside quarry just S. Pitch Coppice       |                        |
| 170                      | 47827283       | U.E.B.                            | small trackside quarry 490 yds N. High Vinnals     | R                      |
| <i>Grid Square 47/73</i> |                |                                   |                                                    |                        |
| 171                      | 47077386       | U.B.B.                            | exposure 970 yds W.N.W. Gorsty                     |                        |
| 172                      | 47157339       | U.E.B.                            | trackside exposure 880 yds W.S.W. Gorsty           |                        |
| 173                      | 47327343       | U.E.B.                            | trackside exposure 700 yds W.S.W. Gorsty           |                        |
| 174                      | 47337353       | L.B.B.                            | trackside exposure 660 yds W.S.W. Gorsty           |                        |
| 175                      | 47337364       | L.B.B.                            | trackside exposure 640 yds W. Gorsty               |                        |
| 176                      | 47627361       | L.B.B.                            | trackside 330 yds W. Gorsty                        |                        |
| 177                      | 47687321       | M.E.B.                            | stream exposure 530 yds S.S.W. Gorsty              |                        |
| 178                      | 47727347       | U.E.B.                            | roadside exposure 280 yds S.W. Gorsty              |                        |
| 179                      | 47727361       | L.B.B.                            | trackside exposure 220 yds W. Gorsty               |                        |
| 180                      | 47797379       | L.B.B.                            | trackside exposure 450 yds W.N.W. Mary Knoll House |                        |
| 181                      | 47807352       | U.E.B.                            | roadside exposure 180 yds S.W. Gorsty              |                        |
| 182                      | 47817328       | M.E.B.                            | stream exposure 410 yds S.S.W. Gorsty              |                        |
| 183                      | 47857332       | M.E.B.                            | stream exposure 350 yds S. Gorsty                  |                        |
| 184                      | 47857354       | U.E.B.                            | roadside exposure 120 yds S.W. Gorsty              |                        |
| 185                      | 47857355       | U.E.B.                            | trackside exposure 100 yds S.W. Gorsty             |                        |
| <i>Grid Square 47/74</i> |                |                                   |                                                    |                        |
| 186                      | 47047401       | W.B.                              | exposure 1050 yds N.W. Gorsty                      |                        |
| 187                      | 47227436       | T.S.                              | stream exposure 1100 yds N.W. Gorsty               |                        |
| 188                      | 47237428       | U.W.B.                            | trackside exposure 970 yds N.W. Gorsty             |                        |
| 189                      | 47487420       | U.W.B.                            | trackside exposure 790 yds N.N.W. Gorsty           |                        |
| 190                      | 47807401       | L.B.B.                            | trackside exposure 590 yds N.W. Mary Knoll House   |                        |
| 191                      | 47927422       | U.W.B.                            | roadside exposure 700 yds N.N.W. Mary Knoll House  |                        |
| <i>Grid Square 48/71</i> |                |                                   |                                                    |                        |
| 192                      | 48577149       | L.L.B.                            | track section 860 yds N.W. Batchcott               |                        |
| 193                      | 48587139       | L.L.B.                            | track section 800 yds W.N.W. Batchcott             |                        |
| 194                      | 48677131       | L.L.B.                            | track section 700 yds W.N.W. Batchcott             |                        |
| 195                      | 48807127       | L.W.B.                            | track section 500 yds N.W. Batchcott               |                        |
| <i>Grid Square 48/72</i> |                |                                   |                                                    |                        |
| 196                      | 48737292       | L.B.B.                            | track section 950 yds N.W. Sunnyhill Cottages      | S                      |
|                          |                | U.E.B.                            |                                                    |                        |
| 197                      | 48887237       | L.L.B.                            | track section 700 yds W.S.W. Sunnyhill Cottages    |                        |
| <i>Grid Square 48/73</i> |                |                                   |                                                    |                        |
| 198                      | 48187338       | M.E.B.                            | stream exposure 300 yds S. Mary Knoll House        |                        |
| 199                      | 48217399       | L.B.B.                            | trackside exposure 400 yds N. Mary Knoll House     |                        |
| 200                      | 48287354       | U.E.B.                            | trackside exposure 150 yds S.S.E. Mary Knoll House |                        |
| 201                      | 48387378       | L.B.B.                            | roadside exposure 250 yds N.E. Mary Knoll House    |                        |
| 202                      | 48397368       | L.B.B.                            | trackside exposure 230 yds E. Mary Knoll House     |                        |
| 203                      | 48417361       | L.B.B.                            | trackside exposure 240 yds E.S.E. Mary Knoll House |                        |



| Locality number          | Grid reference | Stratigraphical divisions exposed | Location                                                    | "S" and "R" localities |
|--------------------------|----------------|-----------------------------------|-------------------------------------------------------------|------------------------|
| 204                      | 48537328       | M.E.B.                            | stream exposure 550 yds S.E. Mary Knoll House               |                        |
| 205                      | 48567381       | L.B.B.                            | roadside exposure 440 yds E.N.E. Mary Knoll House           |                        |
| 206                      | 48587323       | U.E.B.                            | stream exposure 610 yds S.E. Mary Knoll House               |                        |
| 207                      | 48637346       | L.B.B.                            | trackside exposure 480 yds S.E. Mary Knoll House            |                        |
| 208                      | 48657385       | L.B.B.                            | roadside exposure 540 yds E.N.E. Mary Knoll House           |                        |
| 209                      | 48727319       | U.E.B.                            | stream exposure 760 yds S.E. Mary Knoll House               |                        |
| 210                      | 48837312       | U.E.B.                            | stream exposure 900 yds S.E. Mary Knoll House               |                        |
| 211                      | 48887304       | U.D.B.                            | stream exposure 1000 yds S.E. Mary Knoll House              |                        |
| 212                      | 48947392       | L.L.B.                            | roadside exposure 880 yds E.N.E. Mary Knoll House           |                        |
| <i>Grid Square 48/74</i> |                |                                   |                                                             |                        |
| 213                      | 48137406       | U.B.B.                            | trackside exposure 470 yds N. Mary Knoll House              |                        |
| 214                      | 48217429       | U.W.B.                            | roadside quarry 700 yds N. Mary Knoll House                 | R                      |
| 215                      | 48317437       | U.W.B.                            | roadside exposure 790 yds N. Mary Knoll House               |                        |
| 216                      | 48697434       | U.W.B.                            | roadside exposure 940 yds N.N.E. Mary Knoll House           |                        |
| 217                      | 48967437       | U.W.B.                            | roadside quarry 1170 yds N.E. Mary Knoll House              |                        |
| <i>Grid Square 49/70</i> |                |                                   |                                                             |                        |
| 218                      | 49127089       | U.W.B.                            | track section 430 yds N.W. Richard's Castle new church      |                        |
| 219                      | 49417086       | U.W.B.                            | road section 220 yds N. Richard's Castle new church         |                        |
| 220                      | 49477077       | U.W.B.                            | quarry 100 yds N. Richard's Castle new church               | R                      |
| 221                      | 49517083       | U.W.B.                            | roadside section 200 yds N. Richard's Castle new church     |                        |
| 222                      | 49537087       | U.W.B.                            | crossroad section 250 yds N. Richard's Castle new church    |                        |
| 223                      | 49577088       | U.W.B.                            | roadside section 300 yds N.N.W. Richard's Castle new church |                        |
| <i>Grid Square 49/71</i> |                |                                   |                                                             |                        |
| 224                      | 49077140       | L.W.B.                            | track section 400 yds N.N.W. Batchcott                      |                        |
| 225                      | 49157143       | W.B.                              | track section 400 yds N. Batchcott                          |                        |
| 226                      | 49207102       | W.B.                              | quarry at Batchcott                                         |                        |
| 227                      | 49227100       | W.B.                              | roadside exposure at Batchcott                              |                        |
| 228                      | 49257123       | W.B.                              | quarry 200 yds N.N.E. Batchcott                             |                        |
| 229                      | 49427118       | U.W.B.                            | hedge section 610 yds N. Richard's Castle new church        |                        |
| 230                      | 49497124       | U.W.B.                            | roadside section 670 yds N. Richard's Castle new church     |                        |
| 231                      | 49507128       | U.W.B.                            | hedge section 700 yds N. Richard's Castle new church        |                        |
| <i>Grid Square 49/72</i> |                |                                   |                                                             |                        |
| 232                      | 49157229       | L.W.B.                            | track section 450 yds S.W. Sunnyhill Cottages               |                        |
| 233                      | 49267226       | L.W.B.                            | track section 400 yds S.W. Sunnyhill Cottages               |                        |
| 234                      | 49427223       | W.B.                              | track section 330 yds S.S.W. Sunnyhill Cottages             |                        |
| 235                      | 49627263       | L.W.B.                            | track section 200 yds N.E. Sunnyhill Cottages               |                        |
| 236                      | 49877207       | W.B.                              | small quarry 640 yds S.E. Sunnyhill Cottages                |                        |
| 237                      | 49927254       | W.B.                              | track section 270 yds S.W. Starvecrow                       |                        |



| Locality number          | Grid reference | Stratigraphical divisions exposed | Location                                            | "S" and "R" localities |
|--------------------------|----------------|-----------------------------------|-----------------------------------------------------|------------------------|
| <i>Grid Square 49/73</i> |                |                                   |                                                     |                        |
| 238                      | 49127378       | U.L.B.                            | trackside exposure 1100 yds W.S.W. Whitcliffe North |                        |
| 239                      | 49337388       | L.W.B.                            | trackside exposure 860 yds W.S.W. Whitcliffe North  |                        |
| 240                      | 49677307       | L.W.B.                            | track section 630 yds N.N.E. Sunnyhill Cottages     |                        |
| <i>Grid Square 49/74</i> |                |                                   |                                                     |                        |
| 241                      | 49017423       | L.W.B.                            | stream exposure 1100 yds N.E. Mary Knoll House      |                        |
| 242                      | 49377416       | L.W.B.                            | roadside exposure 750 yds W. Whitcliffe North       |                        |
| 243                      | 49407417       | L.W.B.                            | roadside exposure 710 yds W. Whitcliffe North       |                        |
| 244                      | 49527422       | L.W.B.                            | roadside exposure 580 yds W. Whitcliffe North       |                        |
| 245                      | 49597426       | L.W.B.                            | roadside exposure 520 yds W.N.W. Whitcliffe North   |                        |
| 246                      | 49677429       | L.W.B.                            | roadside exposure 440 yds W.N.W. Whitcliffe North   |                        |
| 247                      | 49757401       | W.B.                              | trackside exposure 370 yds S.W. Whitcliffe North    |                        |
| 248                      | 49817431       | L.W.B.                            | roadside exposure 310 yds N.W. Whitcliffe North     |                        |
| 249                      | 49817441       | L.L.B.                            | roadside exposure 1000 yds W. Dinham Bridge         |                        |
| 250                      | 49987423       | W.B.                              | trackside exposure 130 yds N.W. Whitcliffe North    |                        |
| <i>Grid Square 50/72</i> |                |                                   |                                                     |                        |
| 251                      | 50017223       | U.W.B.                            | exposure 640 yds S.E. Sunnyhill Cottages            |                        |
| 252                      | 50157272       | W.B.                              | small quarry 70 yds N.E. Starvecrow                 |                        |
| 253                      | 50187205       | D.C.S.                            | road cutting at Overton                             |                        |
| 254                      | 50237278       | W.B.                              | small quarry 170 yds N.E. Starvecrow                |                        |
| 255                      | 50477293       | U.W.B.                            | track section 500 yds N.E. Starvecrow               | R                      |
| 256                      | 50777293       | D.C.S.                            | hedge exposure S. Hucksbarn                         |                        |
| 257                      | 50887288       | D.C.S.                            | small quarry 130 yds S.E. Hucksbarn                 |                        |
| <i>Grid Square 50/73</i> |                |                                   |                                                     |                        |
| 258                      | 50157388       | W.B.                              | trackside exposure 330 yds S.S.E. Whitcliffe North  |                        |
| 259                      | 50367387       | W.B.                              | trackside exposure 460 yds S.E. Whitcliffe North    |                        |
| 260                      | 50867326       | U.W.B.                            | trackside exposure 300 yds N. Hucksbarn             |                        |
| <i>Grid Square 50/74</i> |                |                                   |                                                     |                        |
| 261                      | 50017445       | L.L.B.                            | roadside quarry 770 yds W. Dinham Bridge            | R                      |
| 262                      | 50057415       | L.W.B.                            | exposure at Whitcliffe North                        |                        |
| 263                      | 50067437       | L.W.B.                            | trackside exposure 700 yds W.S.W. Dinham Bridge     |                        |
| 264                      | 50327449       | L.W.B.                            | trackside exposure 430 yds W.N.W. Dinham Bridge     |                        |
| 265                      | 50407450       | L.W.B.                            | trackside exposure 350 yds W.N.W. Dinham Bridge     |                        |
| 266                      | 50517458       | W.B.                              | quarry 300 yds N.W. Dinham Bridge                   |                        |
| 267                      | 50787462       | W.B.                              | pathside exposure 200 yds N.N.E. Dinham Bridge      |                        |
| 268                      | 50897448       | U.W.B.                            | roadside exposure 200 yds E. Dinham Bridge          |                        |
| <i>Grid Square 51/74</i> |                |                                   |                                                     |                        |
| 269                      | 51047433       | U.W.B.                            | roadside exposure 400 yds E.S.E. Dinham Bridge      |                        |
| 270                      | 51077445       | U.W.B.                            | cellar exposure 400 yds E. Dinham Bridge            |                        |
| 271                      | 51237409       | D.C.S.                            | roadside exposure at Ludford House                  |                        |



## APPENDIX 2 : ADDITIONAL LITHOLOGICAL DATA

(1) *Rock Colour Symbols*

Rock colour terms used in the lithological descriptions of the Wenlockian and Ludlovian divisions in Section III are taken from the Rock Color Chart (1951) of the Geological Society of America. The corresponding rock colour symbols (Munsell notation) are given in the following list :

*Wenlock Shales*

Light olive grey 5Y 6/2  
 Pale olive 10Y 6/2  
 Yellowish grey 5Y 7/2  
 Dark yellowish orange 10YR 6/6  
 Brownish grey 5YR 4/1

*Wenlock Limestone*

Light olive grey 5Y 6/1 5Y 6/2  
 Pale olive 10Y 6/1 10Y 6/2  
 Yellowish grey 5Y 7/2  
 Medium grey N5

*Lower Elton Beds*

Pale olive 10Y 6/2  
 Dark yellowish brown 10YR 4/2  
 Greenish grey 5GY 6/1

*Middle Elton Beds*

Light olive grey 5Y 5/2  
 Yellowish grey 5Y 7/2

*Upper Elton Beds*

Light olive grey 5Y 5/1 5Y 5/2  
 Yellowish grey 5Y 7/2  
 Dark yellowish brown 10YR 4/2

*Lower Bringewood Beds*

Light olive grey 5Y 4/2 5Y 5/1 5Y 5/2 5Y 6/1 5Y 6/2  
 Pale olive 10Y 6/2  
 Medium grey N5

*Upper Bringewood Beds*

Medium grey N6  
 Light olive grey 5Y 5/1 5Y 5/2 5Y 6/1 5Y 6/2 5Y 7/1

*Lower Leintwardine Beds*

Light olive grey 5Y 5/2 5Y 6/2  
 Yellowish grey 5Y 7/2  
 Dark yellowish brown 10YR 4/2

*Upper Leintwardine Beds*

Light olive grey 5Y 5/2 5Y 6/1 5Y 6/2  
 Pale olive 10Y 5/2  
 Pale yellowish brown 10YR 6/2  
 Yellowish grey 5Y 7/2  
 Dark yellowish brown 10YR 4/2

*Lower Whitcliffe Beds*

Medium grey N5  
 Greenish grey 5GY 5/1 5GY 6/1  
 Light olive grey 5Y 5/1 5Y 5/2 5Y 6/1 5Y 6/2  
 Dusky yellow 5Y 6/4

*Upper Whitcliffe Beds*

Pale olive 10Y 6/2  
 Light olive grey 5Y 6/2  
 Dusky yellow 5Y 6/4  
 Dark yellowish brown 10YR 4/2



(2) *Carbonate Determinations*

Determinations of carbonate as against insoluble residues using dilute hydrochloric acid have been made on twelve samples of Wenlockian and Ludlovian rocks from the Ludlow district :

|                                                                                                                                       | % carbonate |
|---------------------------------------------------------------------------------------------------------------------------------------|-------------|
| Wenlock Shales (typical specimen) . . . . .                                                                                           | 25.7        |
| Wenlock Limestone (typical specimen of silty limestone from the lower flaggy part of the formation) . . . . .                         | 54.1        |
| Wenlock Limestone (typical nodular limestone from the upper part of the formation) . . . . .                                          | 66.7        |
| Lower Elton Beds (typical white speckled specimen) . . . . .                                                                          | 42.6        |
| Middle Elton Beds (typical specimen) . . . . .                                                                                        | 7.0         |
| Upper Elton Beds (typical specimen) . . . . .                                                                                         | 13.8        |
| Lower Bringewood Beds (typical calcareous siltstone) . . . . .                                                                        | 18.8        |
| Upper Bringewood Beds (typical crystalline limestone) . . . . .                                                                       | 81.9        |
| Lower Leintwardine Beds (calcareous siltstone) . . . . .                                                                              | 27.1        |
| Lower Leintwardine Beds (shelly limestone band) . . . . .                                                                             | 88.9        |
| Second determination from other sample of above . . . . .                                                                             | 88.6        |
| Lower Whitcliffe Beds (a thinly flaggy siltstone ; could be a less calcareous example from any part of the Whitcliffe Beds) . . . . . | 8.4         |





## EXPLANATION OF PLATES

Plate 1, photograph by J. K. St. Joseph. Plate 2, photograph by V. G. Walmsley. Plates 3 to 7 contain illustrations of all the more important Ludlovian index fossils with the exception of most of the graptolites, only one slab of *Monograptus tumescens* being included. Nearly all the figured specimens, prefixed BM., are in the collections of the British Museum (Natural History), whilst the remainder, prefixed BU, are in the Geology Department, University of Birmingham. Before photographing, the specimens were whitened with ammonium chloride. Photographs by W. T. Dean.

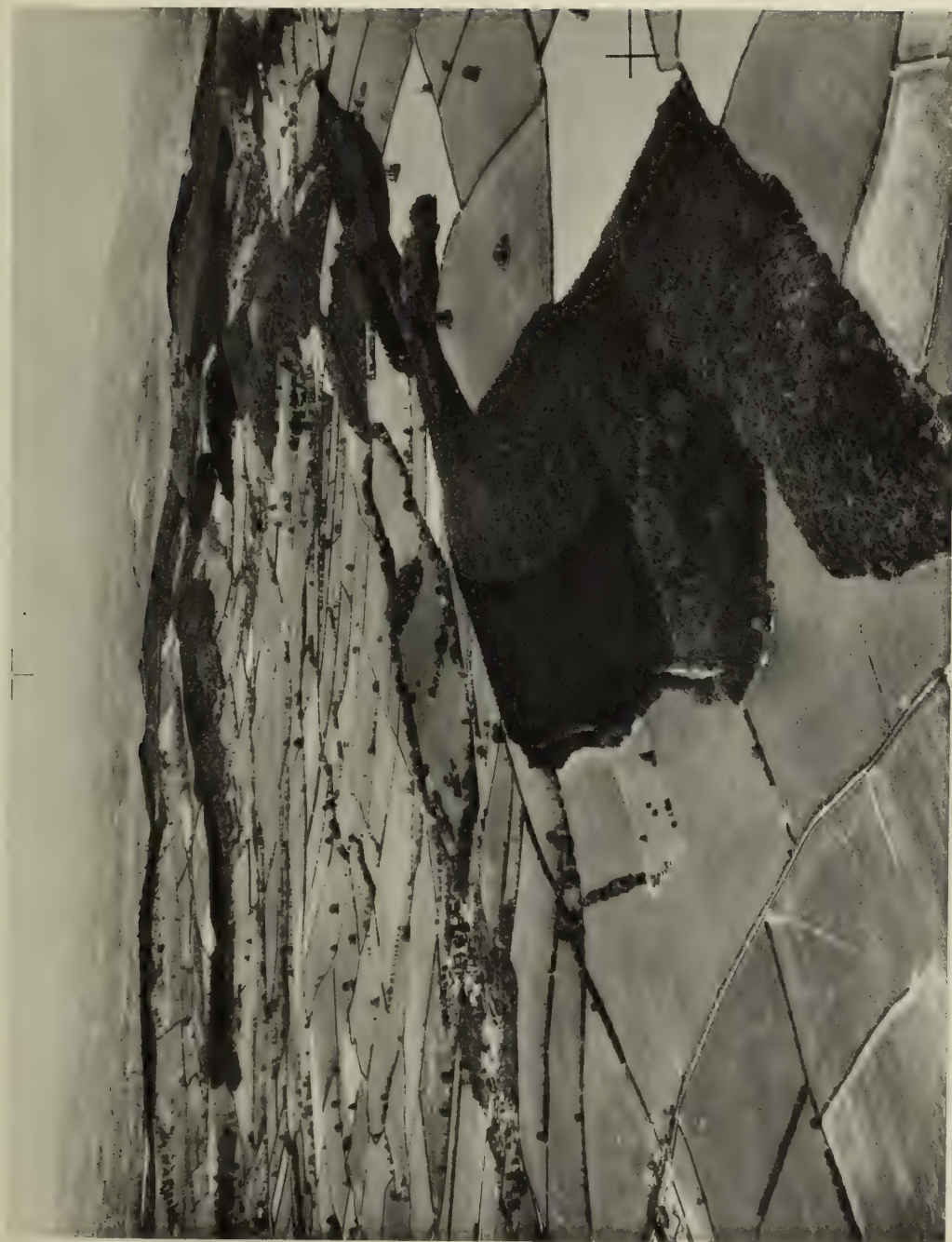
### PLATE 1

Aerial view of the Ludlow Anticline, looking north-eastwards from near Leinthall Earls. The central, low-lying area of Wenlock Shales is bounded on each flank by the parallel, wooded ridges of the Wenlock Limestone and the middle part of the Ludlovian. Lower Bringewood Beds form High Vinnals, the rounded hill with the dark cap of trees, where the dip is east-south-east (i.e. from left to right in the photograph). Bringewood Chase is easily identified by its three wooded summits, of which the western one is formed by Upper Elton Beds and the other two by Lower Bringewood Beds, the dip being northerly into the complementary Downton Syncline. Mary Knoll is the small hill between Bringewood Chase and High Vinnals, and is crowned with a clump of pines; it is formed by limestones of the Upper Bringewood Beds and is almost on the axis of the plunging anticline. Ludlow itself lies beyond the gap.

The more distant view shows the back-slopes of the Ludlovian rocks, dipping south-east off Wenlock Edge under the red marls of Corve Dale. Beyond rises the "whale back" of The Wrekin, formed of Pre-Cambrian volcanic rocks. To the right of centre is the synclinal outlier of Brown Clee Hill, comprising Old Red Sandstone and Carboniferous strata.

From the Cambridge University collection of Aerial Photographs. Photographed by J. K. St. Joseph; copyright reserved.















## PLATE 2

The standard section on the Whitcliffe for the boundary between the Leintwardinian and Whitcliffian Stages (see p. 145 and Text-fig. 14). The head of the hammer indicates the precise position of the boundary, which has been instituted on faunal criteria. A striking lithological change, however, takes place nearly three feet below the junction, at the conspicuous siltstone band indicated by the matchbox. The honeycombed flaggy siltstones below are characteristic of the eastern facies of the Leintwardine Beds, and are sufficiently calcareous for Elles & Slater (1906) to have described them as Aymestry Limestone. When traced westwards into the Leintwardine area they pass laterally into the Mocktree Shale facies. The upper half of the photograph displays clearly the blocky and irregular bedding of the siltstones of the Lower Whitcliffe Beds.

Photograph by V. G. Walmsley.















PLATE 3

*Shaleria ornatella* (Davidson)

FIG. 1. External mould of corrugated variety (No. 24) and two internal moulds of pedicle valves. *Neobeyrichia lauensis* (Kiesow) also present (No. 52). Upper Leintwardine Beds, Locality 27, Wigmore Road. Birmingham University collection BU. 543.  $\times 2$ .

*Chonetes lepisma* (J. de C. Sowerby)

FIG. 2. Pedicle valve showing spine bases. Lower Leintwardine Beds, old quarries north-west of Aymestrey (42226549) BM., BB. 42480.  $\times 4$ .

*Leptostrophia filosa* (J. de C. Sowerby)

FIG. 3. Upper Bringewood Beds, Locality 144, Deepwood. BM., BB. 42481.  $\times 2$ .

FIG. 5. Internal mould of brachial valve (top left) and three internal moulds of pedicle valves. Lower Bringewood Beds, west bank of River Teme 20 yards north of Downton aqueduct bridge (42847292). BM., BB. 42482.  $\times 2$ .

*Strophonella funiculata* (M'Coy)

FIG. 4. External mould of pedicle valve. Upper Bringewood Beds, Locality 22, Bringewood Chase landslip. BM., BB. 42483.  $\times 2$ .

FIG. 6. Internal mould of pedicle valve. Lower Bringewood Beds, Locality 44, Downton Bridge. BM., BB. 42484.  $\times 2$ .

FIG. 7. Internal mould of pedicle valve. Upper Bringewood Beds, Locality 22, Bringewood Chase landslip. BM., BB. 42485.  $\times 2$ .

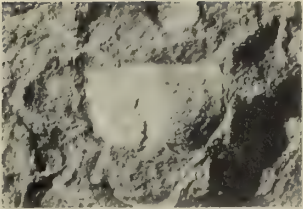
*Strophonella euglypha* (Hisinger)

FIGS. 8, 9. Two views of interior of pedicle valve. Upper Bringewood Beds, Locality 131, Deepwood. BM., BB. 42486.  $\times 1$ .

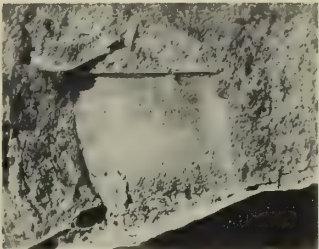




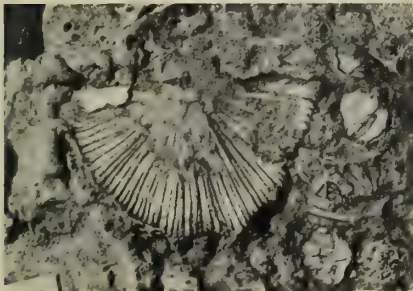
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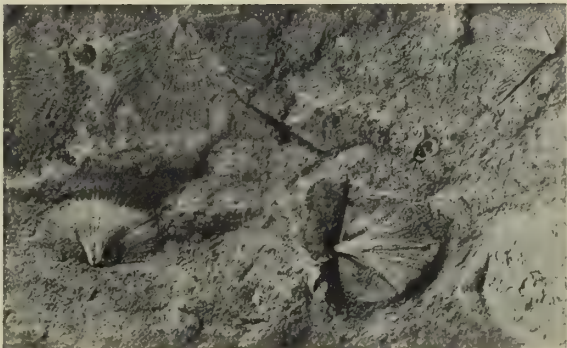
2



3



4



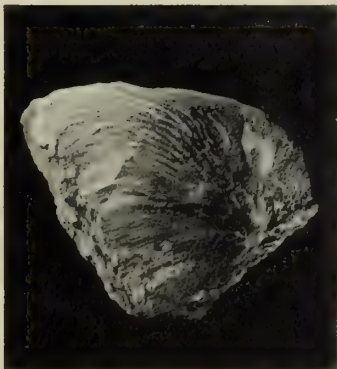
5



6



7



8



9











PLATE 4

*Gypidula lata* Alexander

FIGS. 1, 2, 3. Posterior, ventral and lateral views of internal mould of pedicle valve. Bringewood Beds, roadside  $\frac{1}{2}$  mile north-west of Aymestrey church. BM., BB. 42487.  $\times 1\frac{1}{2}$ .

*Brachyprion* sp. nov.

FIG. 4. Pedicle valve. Lower Bringewood Beds, Locality 208, Mary Knoll House. BM., BB. 42488.  $\times 2$ .

FIG. 5. Internal mould of pedicle valve. Lower Bringewood Beds, Sluvad Wood, Usk inlier (325993). BM., BB. 42489.  $\times 2$ .

*Dayia navicula* (J. de C. Sowerby)

FIGS. 6, 7. Lateral and dorsal views of complete specimen. Lower Leintwardine Beds, track section, Yatton Hill, east of Aymestrey (43196554). BM., BB. 42490.  $\times 2$ .

FIG. 8. Internal moulds of pedicle valves. Lower Leintwardine Beds, small quarry above roadside quarry 700 yards south-east of Trippleton Farm (4144 7299). BM., BB. 42491.  $\times 2$ .

FIG. 11. Internal moulds of brachial and pedicle valves. This slab also includes *Protochonetes ludloviensis* and *Camarotoechia nucula*, thus showing three of the original Ludlovian shelly zone-fossils on the same piece of rock. Lower Whitcliffe Beds, above riverside path, 370 yards north-east of Bow Bridge (4334 7333). BM. BB. 42494.  $\times 2$ .

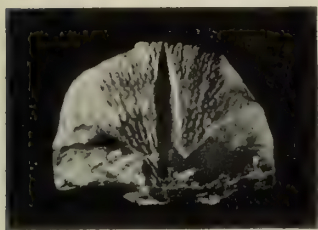
*Leptaena rhomboidalis* (Wilckens)

FIG. 9. Internal mould of pedicle valve. Lower Leintwardine Beds, Locality 25, Wigmore Road. BM., BB. 42492.  $\times 2$ .

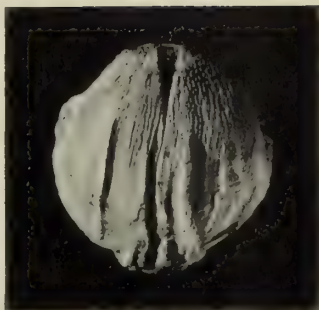
*Conchidium knighti* (J. Sowerby)

FIG. 10. Partly exfoliated valve showing septum of spondylium. Upper Bringewood Beds, View Edge. BM., BB. 42493.  $\times 2/3$ .





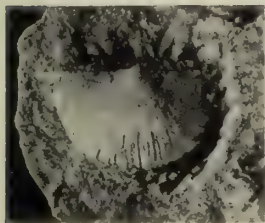
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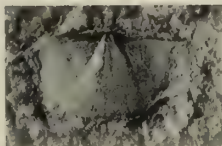
2



3



4



5



6



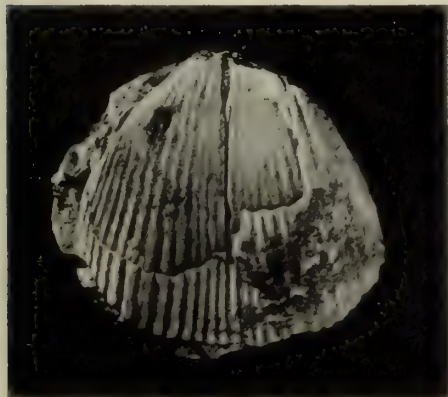
7



8



9



10



11











PLATE 5

*Chonetes lepisma* (J. de C. Sowerby)

FIG. 1. Mostly pedicle valves, interiors and exteriors, some showing spines. Lower Leintwardine Beds, quarry north-west of Aymestrey (42226549). BM., BB. 42495.  $\times 3$ .

*Chonetoidea grayi* (Davidson)

FIG. 2. Internal mould of pedicle valve. Upper Leintwardine Beds, Locality 129, Deepwood. BM., BB. 42496.  $\times 3$ .

*Sphaerirhynchia wilsoni* (J. Sowerby)

FIGS. 3, 6. Dorsal and lateral views of complete specimen. Lower Leintwardine Beds, track section, Yatton Hill, east of Aymestrey (43196554). BM., BB. 42497.  $\times 2$ .

*Atrypa reticularis* (Linnaeus)

FIG. 4. Pedicle valve. Upper Bringewood Beds, Locality 22, Bringewood Chase landslip. BM., BB. 42498.  $\times 1\frac{1}{2}$ .

FIG. 8. Internal mould of pedicle valve. Lower Leintwardine Beds, 280 yards south-east of Fiddler's Elbow (42847568). BM., BB. 42501.  $\times 1\frac{1}{2}$ .

*Leptaena rhomboidalis* (Wilckens)

FIG. 5. Pedicle valve with shell partly abraded near hinge. Lower Bringewood Beds, Locality 19, Wigmore Road. BM., BB. 42489.  $\times 2$ .

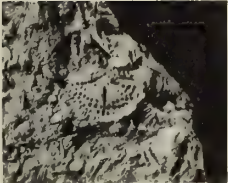
*Howella elegans* (Muir-Wood)

FIG. 7. Mostly pedicle valves. Also shows *Camarotoechia nucula* and *Protochonetes ludloviensis*. Upper Whitcliffe Beds, Locality 56, Castle Bridge, Downton. BM., BB. 42500.  $\times 2$ .

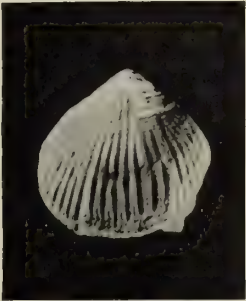




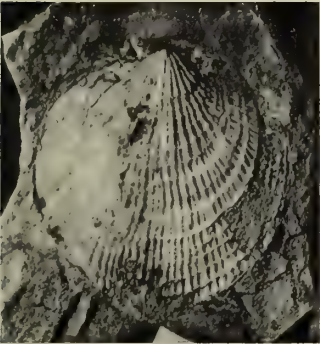
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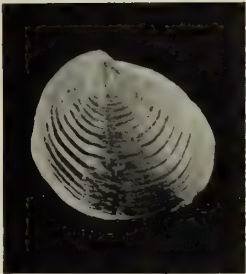
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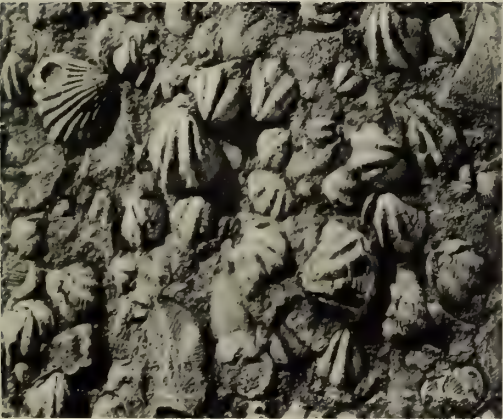
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PLATE 6

*Homalonotus knighti* König

FIG. 1. Internal mould of pygidium. Upper Whitcliffe Beds, north bank of River Teme, 270 yards west of Castle Bridge, Downton (44247423). BM., In. 57168.  $\times 2$ .

*Encrinurus* sp.

FIG. 2. External mould of cranidium. Upper Leintwardine Beds, Locality 26, Wigmore Road. BM., In. 57169.  $\times 2$ .

FIG. 3. External mould of pygidium. Upper Leintwardine Beds, east side of track 480 yards south of Deepwood. BM., In. 57170.  $\times 2$ .

*Calymene neointermedia* (R. & E. Richter)

FIG. 4. Interior of pygidium. Upper Leintwardine Beds, Whitcliffe. BM., In. 57171.  $\times 2$ .

FIG. 7. Internal mould of cranidium. Also shows internal mould of pedicle valve of *Sphaerirhynchia wilsoni*. Upper Leintwardine Beds, lane section 340 yards west-north-west of Caerswall Farm (63703370), Woolhope Inlier. Birmingham University collection BU. 544.  $\times 2$ .

*Acastella* cf. *spinosa* (Salter)

FIG. 5. External mould of cephalon. Upper Whitcliffe Beds, Locality 188, Gorsty. BM., In. 57172.  $\times 2$ .

*Hemiargus* sp.

FIG. 6. External mould of pygidium. Lower Bringewood Beds, Locality 179, Gorsty. BM., In. 57173.  $\times 2$ .

*Dicoelosia biloba* (Linnaeus)

FIG. 8. Internal moulds of pedicle valves. Lower Elton Beds, roadside exposure 200 yards north of Totterton Hall (35958770), Bishop's Castle area. BM., BB. 42503.  $\times 3$ .

*Isorthis orbicularis* (J. de C. Sowerby)

FIG. 9. Internal mould of brachial valve. Lower Leintwardine Beds, 280 yards south-east of Fiddler's Elbow (42847568). BM., BB. 42502.  $\times 2$ .

FIG. 12. Internal mould of pedicle valve. Lower Leintwardine Beds, near Oldfield Farm (46756960). BM., BB. 42506.  $\times 2$ .

*Protochonetes ludloviensis* (Muir-Wood)

FIG. 10. Internal moulds of pedicle (above) and brachial valves. Also internal moulds of pedicle and brachial (bottom left) valves of *Salopina lunata*, brachial valve of *Camarotoechia nucula*, and pedicle valve of *Oribiculoidea rugata*. A typical slab of Upper Whitcliffe Beds, Locality 139, Deepwood. BM., BB. 42504.  $\times 10$ .

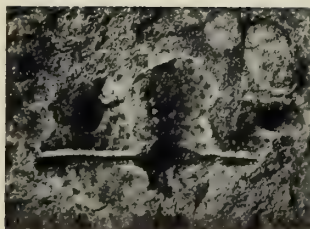
*Lingula lata* (J. de C. Sowerby)

FIG. 11. Lower Leintwardine Beds, lane section 400 yards west-north-west of Todding (41657562). BM., BB. 42505.  $\times 3\frac{1}{2}$ .

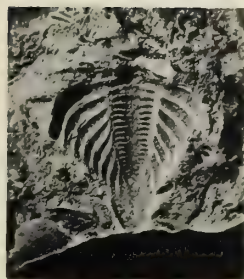




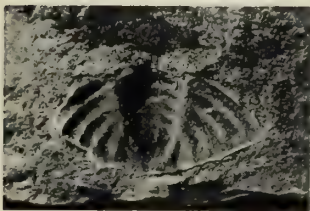
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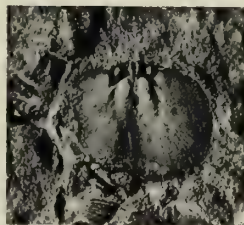
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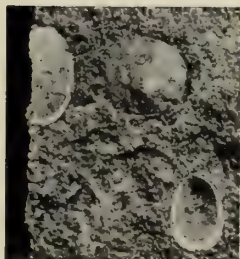
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PLATE 7

*Monograptus tumescens* (Wood)

FIG. 1. Upper Elton Beds, Locality 18, Gorsty. BM., Q. 1328.  $\times 1$ .

*Michelinoceras imbricatum* (Wahlenberg)

FIG. 2. Impression of septum. Whitcliffe Beds, Ludlow. BM., C. 69567.  $\times 1$ .

*Pteronitella retroflexa* (Wahlenberg)

FIG. 3. External mould of left valve. Also shows brachial valve (above) and pedicle valve (below left) of *Salopina lunata*. BM., PL. 3727.  $\times 1\frac{1}{2}$ .

*Nuculites* sp.

FIG. 4. Internal mould of right valve. Also pedicle valve of *Protochonetes ludloviensis* showing spines. Upper Whitcliffe Beds, Locality 214, Mary Knoll House. BM., PL. 3728.  $\times 2$ .

*Fuchsella amygdalina* (J. de C. Sowerby)

FIG. 5. Internal mould of conjoined valves. Whitcliffe Beds, Ludlow. BM., PL. 3729.  $\times 1$ .

*Neobeyrichia lauensis* (Kiesow)

FIG. 6. Internal mould of left valve (male). Temporary exposure, Upper Leintwardine Beds, 690 yards north of New House Farm (45187360). BM., Io. 882.  $\times 5$ .

FIG. 10. Internal mould of right valve (female), showing brood pouch. Upper Leintwardine Beds, Locality 26, Wigmore Road. BM., Io. 883.  $\times 5$ .

*Hemsiella maccoyana* (Jones)

FIG. 7. Internal mould of left valve (male). Lower Bringewood Beds, south-east corner of Elan Aqueduct, Downton Bridge (42907288). BM., Io. 884.  $\times 5$ .

*Beyrichia kloedeni* (M'Coy) var. *torosa* (Jones)

FIG. 8. External mould of left valve (male). Highest Lower Leintwardine Beds, Martin's Shell, Todding (41097543). BM., Io. 885.  $\times 5$ .

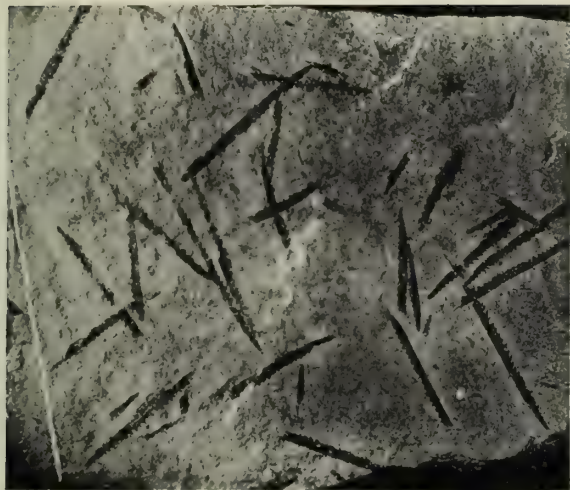
FIG. 11. Latex cast from external mould of right valve (female). Lower Whitcliffe Beds, 270 yards north of Hollybush Cottage (41777328). BM., Io. 887.  $\times 5$ .

FIG. 12. Internal mould of left valve (female). Highest Lower Leintwardine Beds, small quarry above roadside quarry 700 yards south-east of Trippleton Farm (4144 7299). BM., Io. 886.  $\times 5$ .

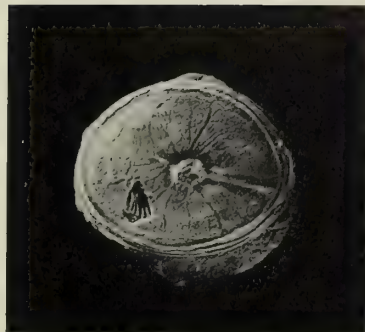
*Serpulites longissimus* (J. de C. Sowerby)

FIG. 9. Whitcliffe Beds, near Woodend Farm (470670). BM., A. 8882.  $\times 1$ .





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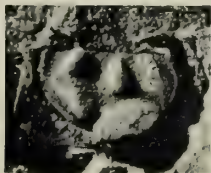
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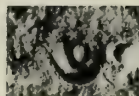
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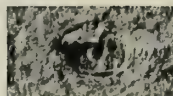
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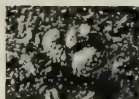
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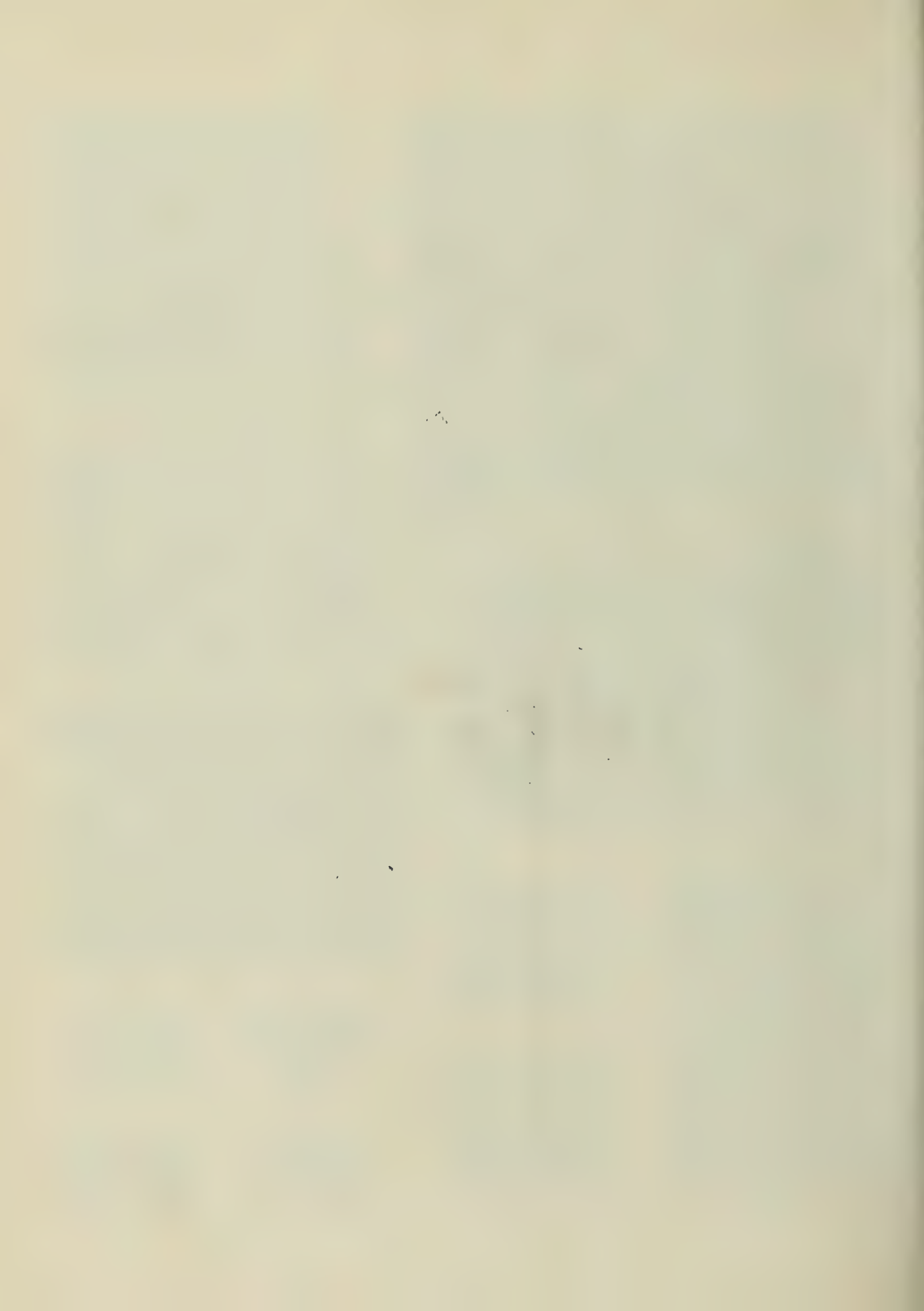


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MIDDLE JURASSIC  
OSTRACODA FROM NORTH  
LINCOLNSHIRE

R. H. BATE

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY Vol. 8 No. 4  
LONDON: 1963







MIDDLE JURASSIC OSTRACODA FROM  
NORTH LINCOLNSHIRE

BY

RAYMOND HOLMES BATE, Ph.D.

*Pp. 173-219 ; 15 Plates ; 15 Text-figures*

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# MIDDLE JURASSIC OSTRACODA FROM NORTH LINCOLNSHIRE

By RAYMOND HOLMES BATE

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## SYNOPSIS

The Bajocian Ostracoda from the Lincolnshire Limestone are described. In a few instances Yorkshire material has been utilized to give a more complete description to some of the Lincolnshire species. They comprise nine families divided into two suborders: Platycopina (one family), Podocopina (eight families). The subfamilies *Pleurocytherinae* and *Schulerideinae* are re-introduced, the subfamilies, *Protocytherinae* and *Schulerideinae*, are given family status, and a new subfamily *Kirtonellinae*, is described. Of the nineteen genera, two subgenera and twenty-two species discussed, six genera, one subgenus and fifteen species are new. The classification of the ostracods belonging to the superfamily Cytheracea is discussed with reference to the Bajocian ostracods. The importance of shape, muscle scars and radial pore canals in this classification is stressed. The variation in the arrangement of the muscle scars has led to the introduction of four types (A-D). A new ostracod hinge, termed *paleohemimerodont*, is described.

## INTRODUCTION

THIS is the first of several papers to be published concerning the marine Middle Jurassic Ostracoda of Yorkshire and Lincolnshire. Not only is there no published work on the Bajocian ostracods of this country, but there has been a general neglect of their study elsewhere. The large number of new genera and species described in the text is a direct reflection of this neglect.

Whilst examining the Bajocian ostracods, morphological details of the carapace



have yielded important information concerning the classification of the ostracod genera (within the Cytheracea) and this suggests that characters at present used to group ostracods at levels higher than the genus should be reviewed. In this respect the importance of the ostracod hinge in the current classification (Moore, 1961) is considered to be out of all proportion to its true value.

As shown by Sylvester-Bradley (1956), the ostracod hinge evolves throughout the Mesozoic, unrelated ostracods often exhibiting identical hinge structures at varying stages in their evolution. Amongst the ostracods examined the simplicity of the duplicature and of the radial pore canals suggests that these structures were developing at a much slower rate than that exhibited by the hinge. As a result, the influence of these two structures on the classification is not strong in the Bajocian.

As there appears to be some variance amongst Jurassic workers as to the precise ammonite zones which go to make up the divisions of the Bajocian Stage, it is proposed to follow Arkell (1956).

All the ostracods described in the present paper are deposited in the collections of the British Museum (Natural History), within the Department of Palaeontology.

#### ACKNOWLEDGEMENTS

The author is indebted to Professor L. R. Moore of Sheffield University in whose department the work embodied in this paper was commenced. The encouragement and guidance so freely given by Professor P. C. Sylvester-Bradley whilst at Sheffield and latterly at Leicester University is also gratefully acknowledged. Dr. C. G. Adams, British Museum (Natural History), kindly made available material collected by himself from the *A. crossi* bed, Kirton Lindsey. The loan of type and comparative material from the following is also recorded: Niedersächsisches Landesamt für Bodenforschung, Hannover (Dr. B. Moos); Smithsonian Institution, United States National Museum, Washington (Dr. G. A. Cooper); Professor P. C. Sylvester-Bradley, Leicester University and Dr. H. V. Howe, Louisiana State University. Dr. H. Dighton Thomas critically read the manuscript. The author also acknowledges the receipt of a D.S.I.R. Research Studentship Grant which made this investigation possible.

#### STRATIGRAPHY AND LOCATION

Ammonites are rarely found in the Middle Jurassic sediments of north-eastern England, and exact age determinations of these beds are difficult. Kent & Baker (1937) record the few ammonites which have been found in the Lincolnshire Limestone and these all occur in the lower 12 ft. This lower division of the Lincolnshire Limestone can be dated accurately on the ammonite evidence as *discites* in age. Arkell (1933: 214) records the presence of *Trigonia hemisphaerica* Lycett in the marly bed situated between the Hibaldstow Oolite<sup>1</sup> and the Kirton Cementstone Series in the region of Kirton Lindsey. This marly bed is the *Acanthothiris crossi* bed from which many of the ostracods described in this paper have been obtained. Arkell notes that this particular species of *Trigonia* is found in the Cotswolds only in the

<sup>1</sup> The Cave and Millepore Oolites referred to in the text are most probably to be correlated with this bed.



Lower Trigonía Grit, a bed of *discites* age. The exact age of the remaining part of the Upper Lincolnshire Limestone is still uncertain. If we consider the *A. crossi* bed to be *discites* in age as suggested by Arkell, it follows that all the ostracods described in this paper are from this single ammonite zone.

A full account of the geology of the Lincoln district is given by Evans (1952), from whom the following succession is adapted :—

|                                     | Thickness<br>in feet |
|-------------------------------------|----------------------|
| Cornbrash . . . . .                 | 3-4                  |
| Blisworth Clay . . . . .            | 20-23                |
| Gt. Oolite Limestone . . . . .      | 19-24                |
| Upper Estuarine Series . . . . .    | 23-28                |
| Upper Lincolnshire Limestone        |                      |
| Hibaldstow Oolite . . . . .         | 35-50                |
| <i>A. crossi</i> Bed . . . . .      | 10-12                |
| Lower Lincolnshire Limestone        |                      |
| Kirton Cementstone Series . . . . . | 8-12                 |
| Blue and Silver Beds . . . . .      | 10-12                |
| Lower Estuarine Series . . . . .    | 0-4                  |
| Northampton Sand . . . . .          | 8-12                 |
| Lias . . . . .                      | 85-90                |

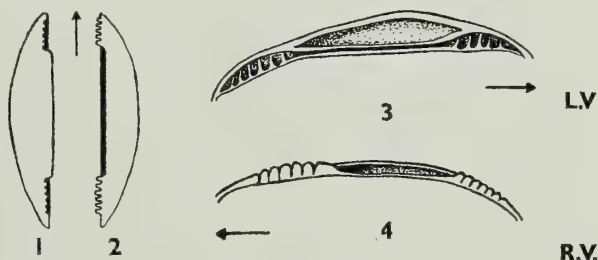
The Lower Lincolnshire Limestone consisting of the Blue and Silver Beds and the Kirton Cementstone Series is perfectly exposed at Greetwell Quarry, due east of Lincoln (map reference TF/002725), where bed by bed sampling was undertaken. The *A. crossi* bed was not exposed in the Greetwell Quarry when the section was examined, although 1 ft. of grey marl at the top of the succession, faunally and lithologically identical with the *A. crossi* bed at Kirton Lindsey, may represent it. Because of the excellence of the material the ostracod fauna of the *A. crossi* bed is described from the Kirton Lindsey section (Kirton Cement Quarry, map reference SE/942011), which was sampled by Dr. C. G. Adams. The Upper Lincolnshire Limestone, apart from the *A. crossi* bed, has so far proven to be almost lacking in ostracods and is not dealt with here. The two localities mentioned in the text, from which additional Bajocian material has been included in this paper are :—Yons Nab headland, Cayton Bay (for the Yons Nab Beds), map reference TA/084844, and Eastfield Quarry, South Cave (for the Cave Oolite and the marl bed beneath), map reference SE/913323. Both localities are in Yorkshire and will be dealt with in more detail in the forthcoming publications.

#### TERMINOLOGY

Terminology concerning the ostracod carapace used in this paper follows that put forward in the *Treatise on Invertebrate Paleontology* (Moore, 1961), with additional hinge terminology (dentate, denticulate, loculate and locellate) taken from Sylvester-Bradley (1956). Where dimorphism has been observed in a species (based on a height : length ratio), the more elongate specimens are regarded as being the males, whilst the shorter specimens are considered to be the females.



A considerable variation exists in the type of hinge exhibited amongst the podocopid ostracods. As a result it has been found convenient to name each distinct type (Moore, 1961: 31-36). Among the species of the new genus *Praeschuleridea*, of which only a single species is described in the present paper, a characteristic hinge is present which is not typically paleomerodont, although at first glance it appears to be so. That type of hinge commonly attributed to the genus *Schuleridea* Swartz and Swain (Triebel, 1954), consists of terminal sockets connected by a median groove in the left valve and terminal teeth connected by a median bar in the right valve, the median bar projecting beyond the hinge line when viewed dorsally. In the hinge of *Praeschuleridea*, however, it is the median element of the left valve which projects beyond the hinge line. In this respect the hinge is typically merodont and in possessing terminal loculate/dentate elements and smooth median elements conforms to the type known as hemimerodont. However, the terminal sockets of the left valve are united across the median bar by a smooth groove. In the right valve a low ridge connects the dentate terminal elements. The hinge is therefore partially hemimerodont and partially paleomerodont, for which the term *Paleohemimerodont* is here proposed (Text-Figs. 1-4).



FIGS. 1-4. Paleohemimerodont hinge. Figs. 1, 2. Dorsal view of left and right valves: note projection of median bar in the left valve beyond the hinge line. Figs. 3, 4. Lateral views, left and right valves.

dont and partially paleomerodont, for which the term *Paleohemimerodont* is here proposed (Text-Figs. 1-4).

#### CLASSIFICATION OF THE BAJOCIAN OSTRACODA

The classification proposed in the *Treatise on Invertebrate Paleontology* (Moore, 1961) is not satisfactory when dealing with the Bajocian ostracods belonging to the superfamily Cytheracea. Indeed the emphasis placed upon hinge structures as a basis for the classification is admitted to result in a purely artificial grouping. The present study has shown that hinge structures are by no means the best form of classifying these animals above the level of a genus.

Although workers such as Gocht & Goerlich (1957) have isolated appendages from fossil ostracod carapaces, it is unlikely that the classification of fossil ostracods will ever follow similar lines to that adopted by zoologists. It will therefore be necessary to look elsewhere for morphological details to provide the taxonomist with the means for developing a more natural classification. The importance of muscle scars, radial pore canals and of the duplicature are recognized in the *Treatise*, but are not



utilized to the full. However, taken in conjunction with general shape (including such functional structure as alae, etc. . . . which are not purely ornamental), these are considered to be of prime importance in the determination of family and subfamily taxa.

The development of such structures as radial pore canals and the duplicature appears to have lagged behind that of the hinge in the evolution of the Cytheracea. An equivalent, well advanced stage of development appears in the muscle scars, which give the impression that these are much more fundamental than the others mentioned above. Their diversity is probably reflected in the appearance of higher taxa (families and subfamilies) in the Bajocian. The development of the numerous genera which occur in the Bajocian sediments commenced in many cases in Liassic times, but there appears to have been a distinct increase in the number of new genera and species during the Bajocian.

The degree of variation shown by the antennal muscle scar(s) is of primary importance in the study of the Bajocian Cytheracea. Only slight variation occurs with respect to the adductor or mandibular scars. The variations exhibited by these centrally situated scars are of four distinct types, although not all these variations are found in the species described here. However, as this is the first of several connected papers, it is convenient to discuss the variations shown by the Bajocian ostracods as a whole.

Within the Cytheracea the basic arrangement consists of four adductor muscle scars situated in a vertical or subvertical row slightly anterior of the valve centre. In front of these scars lies an anterodorsal antennal and an anteroventral mandibular scar. Although it is possible to distinguish four main groupings of these scars it is important to be able to identify the variations which occur within a group. Any natural grouping of characters is almost certainly bound to show some degree of variation and the muscle scars are not without exception.

The position where the muscle fibres are attached to the inside of the carapace is marked by a small upraised spot. If the muscle fibres are attached as a single bundle, a single spot or scar results. However, in some cases, the single scar can be seen to be formed by the fusion of two scars, whilst in the others two distinct antennal scars exist. Both conditions can result either from the splitting of the muscle fibres or by the close proximity of two distinct antennal muscles. In either case there would appear to be only a limited degree of variability possible. It is this variability and the associated types which are discussed below.

### *Type A*

This type approximates most closely to the typical cytheracean muscle scar arrangement in that the adductor scars are situated in a subvertical or vertical row with a single (occasionally two) rounded, anterodorsal antennal scar and a single rounded anteroventral mandibular scar. The antennal scar shows a degree of variation produced by the partial or complete division of the single scar. Complete separation naturally results in the appearance of two distinct scars. Both variants occur in the same species (Text-figs. 6, 7). Partial separation as shown to a slight degree in a single scar of *Pneumatocythere bajociana* sp. nov. results in the develop-



ment of a kidney-shaped scar. Species of *Progonocythere* are liable to possess either a rounded or a kidney-shaped antennal scar. In this type the antennal scar is usually situated anterodorsally, but may vary within a species and sometimes approach the anteromedian position.

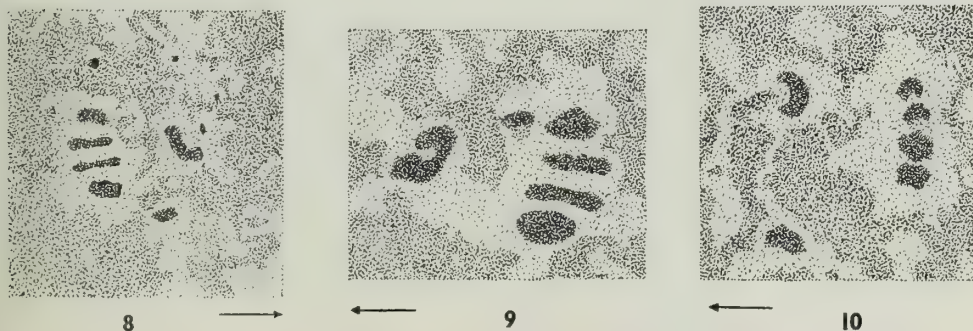


FIGS. 5-7. Type A muscle scar pattern. Fig. 5, *Progonocythere* sp. nov.  $\times 250$ .

Figs. 6 ( $\times 300$ ), 7 ( $\times 200$ ), *Progonocythere bajociana* sp. nov.

### Type B

In a large number of ostracod genera the antennal scar is distinctly crescentic in outline, generally with the opening of the crescent directed anteriorly (Text-fig. 10). Possibly related is the condition where the antennal scar is directed obliquely anterodorsally, a condition somewhat akin to type D described below. The crescentic antennal scar is not considered to be related to the kidney-shaped scar of the previous type (A). A mandibular support spot ("mandibular stutzfleck" of Triebel) is commonly associated with this muscle scar type, and further research may prove this association to be significant.



FIGS. 8-10. Type B muscle scar pattern. Figs. 8 ( $\times 200$ ), 9 ( $\times 320$ ), *Dolococythere maculosa* sp. nov.

Fig. 10, gen. nov.  $\times 240$

### Type C

The most common position for the antennal scar, relative to the adductor scars, appears to be anterodorsal. Amongst several related Bajocian ostracod genera the



antennal scar is decidedly anteromedian in position. It may be either oval or kidney-shaped with a smaller scar in front. Possibly it is the fusion of these two scars which produces the single oval scar. A transitional stage as in type "A" has not been observed. A second feature of this particular type is the position of the adductor muscle scars. In the previous types these scars have formed a vertical or subvertical row on the inside of the valve, only rarely are they situated in a slightly curved row. In the type under discussion here, the adductor scars are distinctly grouped crescentically around the anteromedian antennal scar (Text-figs. 11, 15).

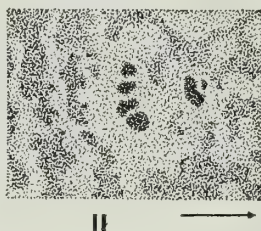
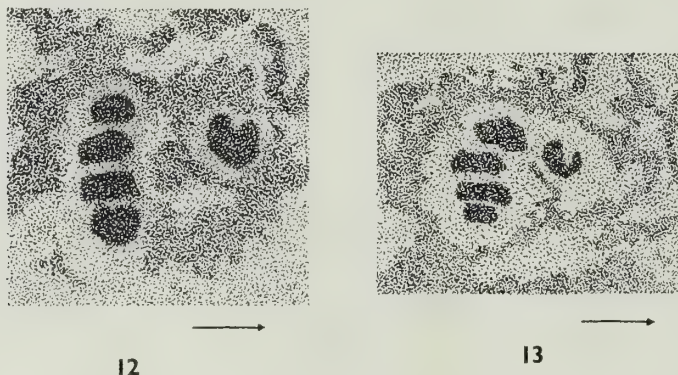


FIG. 11. Type C muscle scar pattern. *Praeschuleridea* sp. nov.  $\times 150$

### Type D

In many Bajocian ostracods the antennal scar is U- or V-shaped with the opening of the scar directed dorsally. The antennal scar may be either anterodorsal or anteromedian in position with the adductor scars in a subvertical row behind, (Text-figs. 12, 13).



FIGS. 12, 13. Type D muscle scar pattern. Fig. 12, *Kirtonella plicata* sp. nov.  $\times 320$   
Fig. 13, *Ektyphocythere triangula* (Brand).  $\times 220$

The mandibular scars show little variation and at the present are not considered to have any distinct role in the ostracod classification.

The variation indicated for the four types of muscle scar arrangement is not exhaustive, although it seems unlikely that any other major group will be found in



the Middle Jurassic ostracods. Evidence so far available suggests that a genus possessing a U-shaped antennal scar should not be placed, for example, in the same family grouping as those possessing a rounded antennal scar. However, it is important that muscle scars should not be used alone in identifying family and subfamily taxa—rather they should be used in conjunction with other characters.

At the moment little is known concerning the importance of the small group of dorsal scars which often occur above the adductor scars (Pl. 12, fig. 10). Although these probably include additional antennal and mandibular scars, further research is required before any definite statements can be made about them.

The radial pore canals in the cytheracean ostracods studied here are simple, generally short and straight, and widely spaced around the anterior and posterior margins. Their importance in the classification lies in their association with other morphological characters, and it is probably only the anterior canals which are of value in this connexion. All related ostracod genera in the Bajocian sediments of north-east England, possess similar radial pore canals, the only variation being in the number present. A basic pore canal arrangement is therefore considered to indicate subfamily or family relationship when taken in conjunction with other characters. In *Schuleridea* Swartz & Swain, *Asciocythere* Swain, and *Praeschuleridea* gen. nov. (here all considered to belong to the same family), the radial pore canals are arranged fan-like around the anterior margin, the only variation being numerical.

The duplicature in the Bajocian ostracods tends to be simple, with the line of concrescence and inner margin coinciding.

In conclusion, the following are considered important in the ostracod classification :

Shape, hinge features, muscle scars, radial pore canals (and associated duplicature), and the presence or absence of an eye tubercle (an eye node and an eye swelling being similar ocular structures but having less prominence on the carapace) are all considered to be important characters in the diagnosis of a genus. For higher taxa all the foregoing characters are of importance with the exception of the hinge and the ocular structures. The three genera quoted previously may be used again in this context: *Asciocythere*, *Schuleridea* and *Praeschuleridea* are three distinct genera possessing different hinge structures but having a similar outline, the same type of muscle scar arrangement, and radial pore canals arranged fan-like around the anterior margin. All three belong to the same family. The characters used above to relate them are emphasized in the classification of the ostracods in the present paper.

#### SYSTEMATIC DESCRIPTIONS

Subclass **OSTRACODA** Latreille, 1806

Order **PODOCOPIDA** Müller, 1894

Suborder **PLATY COPINA** Sars, 1866

Family **CYTHERELLIDAE** Sars, 1866

Genus **CYTHERELLA** Jones, 1849

**DIAGNOSIS.** A genus of Cytherellidae, oval to subrectangular in outline, without ornamentation. A shallow dorsomedian depression. Right valve larger than left.

**TYPE SPECIES.** *Cytherina ovata* Roemer, 1840.



*Cytherella fullonica* Jones & Sherborn

(Pl. 1, figs. 1, 2)

1888. *Cytherella fullonica* Jones & Sherborn, p. 274, pl. 1, fig. 12a-c.

DIAGNOSIS. A subrectangular species of *Cytherella* with an obliquely angled posterodorsal slope.

LECTOTYPE. (chosen here) I. 1857a, a single left valve, figd., Jones & Sherborn, 1888, pl. 1, fig. 12a-c, Blue Fuller's Earth Clay, Midford nr. Bath.

PARALECTOTYPE. I. 1857b, a single left valve, horizon and locality as above.

DESCRIPTION. *Carapace* subrectangular in outline, the right valve being larger than the left which it overlaps on all sides except around the anterior margin. Greatest length through midpoint, greatest height in the anterior third whilst the greatest width is in the posterior third. Anterior broadly rounded, posterior obliquely rounded, dorsal margin slightly concave medially with rounded cardinal angles. The posterodorsal slope is long and obliquely sloping to the posterior. Ventral margin medially concave. Surface of carapace smooth with shallow dorsomedian depression marking position of muscle scars, internally situated on muscle scar node. Internally the right valve has a groove extending around the free margin for reception of the left valve.

*Dimensions*

Io. 522 left valve, length 0.69 mm.; height 0.35 mm. Io. 520 right valve (Pl. 1, figs. 1, 2), length 0.71 mm.; height 0.39 mm.

REMARKS. Over 100 specimens of this species have been examined from the Middle Bajocian, Kirton Shale, Kirton Lindsey and from the Kirton Cementstone Series; Greetwell Quarry, Lincoln.

Genus *CYTHERELLOIDEA* Alexander, 1929

DIAGNOSIS. A genus of Cytherellidae, subrectangular in outline variously ornamented with ridges and swellings. Right valve larger than left.

TYPE SPECIES. *Cytherella williamsoniana* Jones, 1849.

REMARKS. Placed as a subgenus of *Cytherella* by Reyment (1960), but considered here as a distinct genus.

*Cytherelloidea catenulata* (Jones & Sherborn)

(Pl. 1, figs. 3-6)

1888. *Cytherella catenulata* Jones & Sherborn, p. 274, pl. 5, fig. 6a-c.

1948a. ? *Cytherelloidea catenulata* (Jones & Sherborn) Sylvester-Bradley, p. 200, pl. 14, fig. 11, text-fig. 7.

DIAGNOSIS. A species of *Cytherelloidea* with crescent-shaped swelling situated close to posterior margin of valve. Dorsal limb of crescent bending over and curving forwards close to ventral margin to produce a swelling shaped like a question mark.



LECTOTYPE. (chosen here) I. 1876, a single left valve, fig., Jones & Sherborn, 1888, pl. 5, fig. 6a-c. Fuller's Earth Clay, Midford nr. Bath.

PARALECTOTYPES. I. 1846 and Io. 796 a left and right valve. Horizon and locality as above.

DESCRIPTION. *Carapace* subrectangular in outline with a prominent posterior swelling shaped like a question mark. Shell surface ornamented with a reticulate pattern of very fine ridges. Depending on preservation this latter ornamentation may be almost imperceptible. Greatest length of carapace passes through midpoint with the greatest height in the anterior or posterior third. Greatest width in the posterior third. Dorsal margin of both valves slightly concave in the anterior half, becoming strongly convex just behind valve middle. Cardinal angles broadly rounded. Posterodorsal slope oblique. Ventral margin medially concave. Anterior broadly rounded, posterior rounded tending to be rather flattened terminally. Right valve larger than the left which it overlaps on all sides except around the anterior margin where the right valve merely overreaches the left. A dorsomedian depression marks the position of the muscle scars, which (as imperfectly seen) are typical of the family.

#### *Dimensions*

Io. 524. left valve (Pl. 1, figs. 3, 5), length 0.75 mm; height 0.37 mm. Io. 525 right valve (Pl. 1, figs. 4, 6), length 0.79 mm; height 0.44 mm.

REMARKS. 50 specimens of *C. catenulata* have been obtained from the Kirton Shale, Kirton Lindsey and from the Kirton Cementstone Series, Lincoln.

### Genus *PLATELLA* Coryell & Fields 1937

DIAGNOSIS. A genus of Cytherellidae, oval to subrectangular in outline, finely or coarsely pitted, with shallow dorsomedian sulcus. Right valve larger than left.

TYPE SPECIES. *Platella gatunensis* Coryell & Fields, 1937.

#### *Platella jurassica* sp. nov.

(Pl. 1, figs. 7-10)

DIAGNOSIS. A species of *Platella* strongly ovoid in outline with arched dorsal margin and strongly concave ventral margin. Surface of carapace typically ornamented with a reticulate pattern of small pits arranged in rows, rows paralleling sides of carapace.

HOLOTYPE. Io. 526, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 527, Io. 797-98, horizon and locality as above.

DESCRIPTION. *Carapace* ovoid in outline with a strongly arched dorsal margin and a strongly concave ventral margin. Anterior broadly rounded with a narrow compressed rim, posterior rather obliquely rounded. Carapace characteristically ornamented with a reticulate pattern of small pits arranged in rows paralleling the sides of the carapace. Greatest length through midpoint, greatest height in



the anterior third, whilst the greatest width is just behind valve centre. Right valve larger than the left, which it overlaps along the dorsal and ventral margins but not around the anterior and posterior margins. A distinct dorsomedian pit marks the position of the muscle scars. Internal details not known.

### *Dimensions*

HOLOTYPE. Io. 526 carapace (Pl. 1, figs. 7-10), length 0.64 mm. ; height 0.37 mm. ; width 0.23 mm.

PARATYPE. Io. 527 right valve, length 0.43 mm. ; height 0.28 mm.

REMARKS. This species differs from the Miocene *P. gatunensis* Coryell & Fields (1937, Text-fig. 2a, b) in the possession of a more strongly concave ventral margin and in the smaller size of the pits. Only a few specimens of this species have been found from Kirton Lindsey and apart from the two described, were poorly preserved.

Suborder **PODOCOPINA** Sars, 1866

Superfamily **CYPRIDACEA** Baird, 1845

Family **PARACYPRIDIDAE** Sars, 1923

Genus **PARACYPRIS** Sars, 1866

DIAGNOSIS. An elongate genus of the Paracyprididae, posteriorly acuminate. Dorsal margin arched, ventral margin incurved. Anterior and posterior vestibules well developed, anterior radial pore canals branching. Muscle scars an oblique row of three scars with two or more behind. Left valve larger than right.

TYPE SPECIES. *Paracypris polita* Sars, 1866.

*Paracypris bajociana* sp. nov.

(Pl. 2, figs. 1-8)

DIAGNOSIS. Carapace sub-reniform, dorsal margin strongly convex. Left valve overlapping the right along antero-, and posterodorsal slopes. Anterior and posterior cardinal angles not strongly developed. Ventral margin slightly concave. Greatest length ventral of midpoint. Anterior radial pore canals branching and evenly spaced.

HOLOTYPE. Io. 528, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 529-33, Io. 694, Io. 799-802, horizon and locality as above, and from the marl bed below the Cave Oolite, Eastfield Quarry, South Cave.

DESCRIPTION. *Carapace* sub-reniform in outline, rather elongate. Anterior broadly rounded ; posterior tapering. Dorsal margin convex with a slight break at the anterior and posterior cardinal angles. Anteriorly there is a short antero-dorsal slope, whilst posteriorly there is a longer, much steeper slope which extends down to the extreme posterior, close to the ventral margin. The latter more strongly concave in the right valve than in the left. Greatest height and width in the anterior third. Greatest length below midpoint. Shell surface smooth. Left valve larger



than the right, overlapping most strongly along the anterodorsal and posterodorsal margins and midventrally with only slight overlap around the anterior margin. *Muscle scars* as seen from the exterior consist of an oblique row of three oval scars with two other scars behind. *Radial pore canals* long, branching anteriorly, straight posteriorly. Anteriorly the pore canals are evenly spaced around the margin, in which character they appear to differ from the type species: *Paracypris polita* Sars. Anteriorly there are 6–10 rather thick, main canals which terminally split up into 2, 3, or more fine, hair-like canals. Posteriorly the canals are unbranched and are approximately 10 in number. *Inner margin* and *line of concrescence* do not coincide terminally, an anterior and posterior vestibule being developed. The selva is prominent around the free margin. The *hinge* consists of a simple, long, straight groove in the left valve into which the dorsal edge of the right valve fits.

### Dimensions

HOLOTYPE. Io. 528 carapace (Pl. 2, figs. 1, 3, 4), length 0.60 mm.; height 0.28 mm.; width 0.23 mm.

### PARATYPES

Io. 529 left valve (Pl. 2, fig. 2) length 0.61 mm.; height 0.27 mm.

Io. 530 left valve (Pl. 2, fig. 7) length 0.56 mm.; height 0.25 mm.

Io. 531 left valve length 0.60 mm.; height 0.25 mm.

Io. 532 left valve (Pl. 2, figs. 5, 6) length 0.59 mm.; height 0.27 mm.

Io. 533 left valve (Pl. 2, fig. 8) length 0.57 mm.; height 0.25 mm.

Io. 694 right valve length 0.60 mm.; height 0.25 mm.

REMARKS. *P. bajociana* resembles *P. projecta* (Peterson, 1954, Pl. 17, figs. 14, 15) but differs in having a much stronger overlap of the right valve by the left along the antero- and posterodorsal slopes. The Tertiary *P. aerodynamica* (Oertli, 1956, pl. 1, figs. 24–26, 28–30) is similar in shape, but differs in size (length 1.01 mm.–1.19 mm.) and in its more strongly branching anterior radial pore canals. *P. bajociana* is a common ostracod within the marine Middle Bajocian sediments of Lincolnshire and Yorkshire.

## Superfamily BAIRDIACEA Sars, 1888

### Family BAIRDIIDAE Sars, 1888

#### Genus BAIRDIA McCoy, 1844

DIAGNOSIS. A genus of Bairdiidae elongate to subtriangular in outline. Dorsal margin arched, antero- and posterodorsal slopes usually concave, sharply inclined. Ventral margin strongly convex antero-, and posteroventrally. Posterior acuminate, slightly upturned. Duplicature broad, vestibules well developed. Muscle scars in a rosette, approximately 9 in number. Left valve larger than right.

TYPE SPECIES. *Bairdia curtus* McCoy, 1844.



*Bairdia hilda* Jones

(Pl. 2, figs. 9-12; Pl. 3, figs. 1-4)

1884. *Bairdia hilda* Jones, p. 771, pl. 34, fig. 20.1888. *Bairdia fullonica* Jones & Sherborn, p. 253, pl. 5, fig. 4a-c.1948a. *Bairdia* cf. *hilda* Jones; Sylvester-Bradley, p. 199, text-fig. 5.

DIAGNOSIS. A species of *Bairdia*, subdeltoid in outline, strongly convex in dorsal view. Dorsal margin high, dorsal slopes steeply inclined. Posterior acuminate, upturned. Shell surface finely punctate.

LECTOTYPE. IN. 41951, a single left valve figd. Jones, 1884, pl. 34, fig. 20, Gt. Oolite; Richmond Boring, (London) at a depth of 1205 feet.

DESCRIPTION. *Carapace* subdeltoid in side view. Surface smooth with extremely fine puncta. Left valve larger than the right which it strongly overlaps midventrally and along the dorsal margin, particularly in the region of the cardinal angles. Anteriorly there is no overlap, posteriorly there may be very slight overreach along the posteroventral margin. Although the specimens vary slightly, the general outline is similar for all the specimens examined. Dorsal margin convex in the left valve, straight or very slightly convex in the right. Ventral margin strongly concave in the right valve, only slightly concave in the left, the latter being overhung by the ventrolateral border. Anterior rounded with a distinct anterodorsal slope; straight or slightly convex in the left valve, concave in the right. Posterior margin convex posteroventrally, although the degree of convexity varies in individual specimens. Posterodorsal margin straight, upturned at extreme posterior, more sharply pronounced in the right valve. Anterior and posterior cardinal angles sharply defined. *Muscle scars* consist of a rosette of 8 scars with a single central scar (Pl. 3, fig. 4). The downset dorsal edge of the right valve forms the hinge by fitting into the shallow groove of the left valve, the groove being terminally deepened to form socket-like terminations. Dorsal to this groove is an elongate shelf-like accommodation groove. *Inner margin* and *line of concrescence* terminally do not coincide, the vestibules being particularly well developed along the anteroventral and posteroventral margins. The selvage is distinct around the free margin, obliquely cutting across the anterior and posterior borders. In well preserved specimens a broad flange is developed around the posteroventral and anteroventral margins.

*Dimensions*

Io. 534 internal cast (Pl. 3, fig. 4), length 0.93 mm.; height 0.53 mm.; width 0.53 mm.

Io. 535 carapace (Pl. 2, figs. 9, 11, 12), length 0.99 mm.; height 0.56 mm.; width 0.43 mm.

Io. 536 left valve (Pl. 3, figs. 2, 3), length 0.99 mm.; height 0.56 mm.

Io. 537 right valve (Pl. 2, fig. 10, pl. 3, fig. 1), length 0.95 mm.; height 0.49 mm.

REMARKS. The specimen described by Jones (1884) as *B. hilda* and by Jones & Sherborn (1888) as *B. fullonica* were regarded as conspecific by Sylvester-Bradley (1948a), when he showed a range of variation between the two. This is in agreement



with the present work, as the specimens described do not fall definitely into *B. hilda* or *B. fullonica*, but have characters which may be found in either. The specimens described here are abundant in the Middle Bajocian Kirton Shale, Kirton Lindsey and in the Kirton Cementstone Series, Lincoln.

Superfamily **CYTHERACEA** Baird, 1850

Family **BYTHOCYTHERIDAE** Sars, 1926

Genus **MONOCERATINA** Roth, 1928

**DIAGNOSIS.** A subrectangular genus of Bythocytheridae. Dorsal margin long and straight, terminating in a slight caudal process. Right valve with dorsal groove for reception of hinge bar of the left. Median sulcus shallow with a prominent swelling below and behind, sometimes bearing a strong spine. Muscle scars an oblique row of 4 or 5 scars.

**TYPE SPECIES.** *Monoceratina ventrale* Roth, 1928.

***Monoceratina vulsa*** (Jones & Sherborn)

(Pl. 3, figs. 5-12)

1888 *Cytheridea vulsa* Jones & Sherborn, p. 263, pl. 2, fig. 4a-b.

1938 *Monoceratina vulsa* (Jones & Sherborn) Triebel & Bartenstein, p. 516, pl. 3, figs. 17, 18.

?1955 *Bythocythere aliena* Ljubimova, p. 34, pl. 2, fig. 3a-b.

1960 *Monoceratina cf. vulsa* (Jones & Sherborn); Lutze, p. 433, pl. 37, fig. 5a-b.

**DIAGNOSIS.** A strongly convex species (in dorsal view) of *Monoceratina* distinctly ornamented with elongate pits, the latter producing low irregular ridges.

**LECTOTYPE.** (chosen here) I. 1842, a single left valve figd. Jones & Sherborn, 1888, pl. 2, fig. 4a-b. Gt. Oolite; Richmond Boring (London) at a depth of 1205 feet.

**DESCRIPTION.** *Carapace* subquadrate in side view with a broad posteroventral border. In dorsal view, almost parallel-sided, diverging slightly to the posterior. Sexual dimorphism suggested by the presence of a more elongate specimen, possibly the male. Hinge line straight, terminating at the anterior cardinal angle in a small node, reminiscent of an eye swelling. Ventral margin slightly convex. Anterior uniformly rounded, posterior acuminate, produced by a long, oblique, strongly convex posteroventral slope and a short, slightly concave posterodorsal slope. Carapace strongly convex, divided into two subequal lobes by a vertical median sulcus. The anterior lobe, in dorsal view, is not so enlarged as is the posterior lobe and is uniformly rounded anteriorly. The posterior lobe follows the outline of the carapace in having a strong posteroventral upward sweep, at the extreme posteroventral corner of which there is a prominent swelling. A short longitudinal furrow, most strongly developed in the supposed male dimorph, bisects the posterior border along the line of greatest length, the latter being dorsal of midpoint. Greatest height just behind valve middle, greatest width below and posterior of the median sulcus. Valves almost equivalve, although the left valve slightly overlaps the right at the



centre of the ventral margin and at the posterior cardinal angle. A distinct postero-ventral keel is produced by the shelf-like marginal border, continued ventrally as a slight ridge. The anterior marginal border is thus continuous with the postero-ventral border along the ventral margin. Shell surface entirely covered by distinct pits producing low, irregular ridges, the whole appearing wrinkled. *Internal characters* only observed in the lectotype where the duplicature is broad and the hinge bar can be seen to be produced by the downset dorsal margin of the valve.

#### *Dimensions*

Io. 539 female? carapace (Pl. 3, figs. 5, 6, 8, 10), length 0.65 mm. ; height 0.33 mm. ; width 0.33 mm.

Io. 540 male? carapace (Pl. 3, figs. 7, 9, 11, 12), length 0.68 mm. ; height 0.32 mm. ; width 0.23 mm.

REMARKS. 38 specimens (all complete carapaces) have been recovered from the Kirton Shale, Kirton Lindsey, and the Kirton Cementstone Series, Lincoln.

#### *Monoceratina* sp. cf. *M. scrobiculata* Triebel & Bartenstein

(Pl. 4, figs. 1-4)

DESCRIPTION. *Carapace* elongate quadrate. Dorsal margin long and straight ventral margin short, paralleling the dorsal margin. Anterior broadly rounded, posterior acuminate, broadly triangular. Posterodorsal slope short and slightly concave in the left valve, slightly convex in the right, posteroventral slope long and straight. Anterior and posterior margins compressed. Surface of carapace covered with small pits. At the posteroventral border of each valve a prominent inflation projects strongly downwards and backwards. Valves convex with a vertical median sulcus dividing the carapace into two lobes of which the posterior is the most strongly developed. Greatest length dorsal of midpoint, greatest height in the anterior third, greatest width in the posterior third. A "V" shaped flattened area is present on the ventral surface, delimited laterally by the posteroventral projections. Medially along this flattened area a slight keel is produced by the overlap of the right valve by the left. This overlap along the ventral margin is the only overlap noticed in the specimens here described.

#### *Dimensions*

Io. 538 juvenile carapace. (Pl. 4, figs. 1-4.) length 0.28 mm. ; height 0.13 mm. ; width 0.13 mm. (+ ventrolateral extension).

REMARKS. The two specimens found in the Kirton Shale, Kirton Lindsey, are similar in some respects to *M. scrobiculata* Triebel & Bartenstein (1938, pl. 1, fig. 5a-b, pl. 2, fig. 6). As the best preserved specimen is a juvenile, exact identification with *M. scrobiculata* cannot be made.



Family **PROGONOCYTHERIDAE** Sylvester-Bradley, 1948

REMARKS. For diagnosis see Moore (1961 : Q322), where the family is, however, considered to be strictly artificial in that two subfamilies placed therein (Progonocytherinae and Protocytherinae), are simply groupings of ostracod genera related only by the possession of similar hinge structures. In the present paper the subfamily Protocytherinae is removed from the family and the subfamily Pleurocytherinae restored with subfamily rank. The importance of the hinge structure is no longer maintained for the family (or subfamilies), the artificial nature of which is considered to have been removed.

## Subfamily PROGONOCYTHERINAE Sylvester-Bradley, 1948

EMENDED DIAGNOSIS. As for Malz, 1961 : 176, not Howe *in* Moore, 1961 : 326.

REMARKS. The ostracod genera included here are related by the following characteristics : carapace subquadrate in outline, often tapering to the posterior with a tendency for the ventrolateral part of the carapace to overhang the ventral surface. Internally the inner margin and line of concrescence coincide, there being no suggestion that a vestibule is present. The radial pore canals are straight and simple, few in number and widely spaced around the anterior and posterior margins. The muscle scars consist of a subvertical row of 4 rounded or oval adductor scars with an anterodorsal antennal scar which may be either rounded or weakly kidney-shaped. The mandibular scar is anteroventral in position and is also rounded. The muscle scar pattern is therefore of type A, as described previously (p. 180).

Genus **PROGONOCYTHERE** Sylvester-Bradley, 1948

EMENDED DIAGNOSIS. A subrectangular genus of Progonocytherinae, often strongly dimorphic. Carapace tapering posteriorly, dorsal margin noticeably angled in female dimorphs. Lateral border overhanging ventral surface. Shell variously ornamented. Hinge entomodont. Left valve larger than right.

TYPE SPECIES. *Progonocythere stilla* Sylvester-Bradley, 1948.

***Progonocythere cristata*** sp. nov.

(Pl. 4, figs. 5-15 ; pl. 5, figs. 1-6)

DERIVATION OF NAME. Latin ; *cristatus*, crested.

DIAGNOSIS. A species of *Progonocythere* with strong keel-like extension of ventrolateral margin ; shell surface punctate ; anterior and posterior marginal areas compressed.

HOLOTYPE. Io. 543, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 544-50 and Io. 803-05, horizon and locality as above.

DESCRIPTION. *Carapace* oval in outline, rather swollen medially. Sexual dimorphism apparent, presumed males being the more elongate in outline. Dorsal



margin slightly convex, sloping to the posterior; cardinal angles distinct. Ventral margin convex; anterior broadly rounded, posterior triangular with a concave posterodorsal slope and a convex posteroventral slope. Anterior and posterior borders compressed. A slight swelling at the anterior cardinal angle is suggestive of an eye swelling. The ventrolateral margin of each valve projects strongly below the ventral surface in the form of a strong keel. Shell surface punctate, but depending on preservation may appear smooth. Ventral surface of each valve ornamented with about three longitudinal ridges. Weak longitudinal ridges occur in juvenile instars along the ventrolateral border; these are occasionally weakly developed in the adults. Left valve larger than the right, projecting strongly above the right along the dorsal margin, slightly overlapping the right valve midventrally. Greatest length through midpoint, greatest height in the anterior third, greatest width just posterior of valve centre. Hinge *entomodont*: right valve with terminal dentate ridges possessing 7 anterior and 7 posterior teeth; median groove strongly loculate, expanded anteriorly, the ventral edge of the expanded part being distinctly dentate. Left valve with terminal loculate sockets and a dentate median bar, more coarsely dentate anteriorly. Free margin formed by a prominent ridge (the selvage), external to which is a narrow flange, only clearly observable around the anterior and ventral margins. Midventrally a narrow "lip" is developed just below and posterior of the ventral incurvature in the right valve. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* straight and widely spaced, approximately 8 anteriorly, not seen posteriorly. Muscle scars consist of a crescent of 4 oval adductor scars with a large, rounded anterodorsal antennal scar and a rounded anteroventral mandibular scar. Young instars possess antimerodont hinges.

### *Dimensions*

HOLOTYPE. Io. 543 female carapace (Pl. 4, figs. 5-8) length 0.63 mm.; height 0.40 mm.; width 0.36 mm.

### PARATYPES

Io. 544 male carapace (Pl. 4, figs. 9, 10) length 0.69 mm.; height 0.43 mm.; width 0.35 mm.

Io. 545 right valve male, (Pl. 5, fig. 5) length 0.71 mm.; height 0.44 mm.

Io. 546 left valve female (Pl. 4, fig. 11, Pl. 5, fig. 6) length 0.59 mm.; height 0.40 mm.

Io. 547 "juv." female carapace (Pl. 4, figs. 12, 13) length 0.44 mm.; height 0.15 mm.; width 0.27 mm.

Io. 548 "juv." male carapace (Pl. 4, figs. 14, 15, Pl. 5, figs. 3, 4) length 0.48 mm.; height 0.27 mm.; width 0.27 mm.

Io. 549 right valve male (Pl. 5, fig. 1) length 0.67 mm.; height 0.37 mm.

Io. 550 female carapace (Pl. 5, fig. 2) length 0.61 mm.; height 0.40 mm.; width 0.33 mm.

REMARKS. *Progonocythere cristata* differs from the type species, *P. stilla* Sylvester-Bradley (1948 pl. 12, figs. 1, 2, pl. 13, figs. 1, 2) in the possession of a sharpened keel-like extension of the ventrolateral border of the carapace, and in being more



distinctly acuminate posteriorly. The species is common in the type locality and in the Kirton Cementstone Series, Greetwell Quarry Lincoln. Young instars (already dimorphic) in all samples greatly outnumber adults.

Genus **PNEUMATOCY THERE** nov.

DERIVATION OF NAME. Greek, *πνεῦμα*, -*atos* "full of air or blown up", + *cythere*.

DIAGNOSIS. Progonocytherinae, strongly convex in dorsal view, a distinct lateral swelling extending slightly below ventral surface in side view, particularly posteroventrally. Marginal areas slightly compressed, oblique furrow commonly present below and behind anterior cardinal angle. Muscle scars a subvertical row of 4 oval adductor scars with single (occasionally 2 small scars), large anterodorsal antennal scar, and smaller rounded anteroventral mandibular scar. Radial pore canals straight, diverging slightly outwards away from the valve midline, few in number, and widely spaced. Inner margin and line of concrescence coincide. Normal pore canals large and rounded. Hinge antimerodont. Left valve larger than right which it overlaps evenly along ventral margin, and region of anterodorsal and posterodorsal slopes. Shell surface variously ornamented.

REMARKS. This genus, whose species are large, is not easily confused with any other known Bajocian ostracod. In shape, however, it is similar to *Progonocythere* Sylvester-Bradley from which it can be distinguished by its strongly convex carapace and in the possession of an antimerodont hinge. The normal pore canals in the type species are much larger than any exhibited by species of *Progonocythere*.

TYPE SPECIES. *Pneumatocythere bajociana* sp. nov.

***Pneumatocythere bajociana*** sp. nov.

(Pl. 5, figs. 7-10; Pl. 6, figs. 1-10; Pl. 7, figs. 1-4; Text-figs. 6, 7)

DIAGNOSIS. A large species of *Pneumatocythere* characterized by weakly reticulate ornamentation of transverse and longitudinal ridges. This ornamentation may be absent owing to the state of preservation, in which case the rather large, circular normal pore canals are strongly visible.

HOLOTYPE. Io. 551, Yons Nab Beds, Cayton Bay, Yorkshire.

PARATYPES. Io. 552-557 and Io. 806-814 horizon and locality as above but including the marl bed beneath the Cave Oolite, South Cave, Yorkshire and the Kirton Cementstone Series, Lincoln.

DESCRIPTION. *Carapace* oval in outline with sexual dimorphism apparent, presumed males being the more elongate. Greatest length extending through midpoint, greatest height at the centre of the carapace in the female, slightly behind centre in the male. The carapace shows a marked degree of inflation, the greatest width being at or slightly behind the valve centre. The ventrolateral border of each valve is strongly convex, projecting slightly below the ventral surface, particularly midventrally. Marginal borders compressed. Anteriorly an oblique



furrow extends from the anterior cardinal angle towards the anteroventral margin. Shell surface ornamented by weakly developed longitudinal ridges, most strongly developed along the lateral border, and weak transverse ridges: the whole producing a weak reticulation. Depending upon preservation the ornament may be lacking completely, in which case the rather large, circular normal pore canals are distinctly visible, evenly spaced over the valve surface. *Left valve* larger than the right which it strongly overreaches along the dorsal margin and around the anterior margin. Posteriorly the right valve tends slightly to overreach the left. Ventrally the left valve slightly overlaps the right. Dorsal margin strongly convex in the left valve with indistinct cardinal angles. In the *right valve* the dorsal margin is not so strongly convex and as in the left valve the posterior cardinal angle is the most strongly developed. Anterior broadly rounded, posterior triangular with a strongly concave posterodorsal slope and a convex posteroventral slope. Ventral margin convex with an anteromedian incurvature. *Hinge* antimerodont with, in the left valve, terminal loculate sockets and a median denticulate bar, above which there is a distinct elongate accommodation groove. In the right valve the terminal elements of the hinge bear from 5 to 6 teeth, the median groove being locellate. The *muscle scars* consist of a subvertical row of 4 adductor scars situated anteriorly of the valve centre. The large, oval antennal scar is situated anterodorsally, although this may vary, the scar approaching anteromedian. The single antennal scar appears to be formed by the fusion of two smaller scars (pl. 7, fig. 2). The mandibular scar is rounded and situated anteroventally to the adductor scars. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* rather thick, straight, diverging away from midline. Anteriorly there are 9 canals, 5 of which are placed below midline. Posteriorly there are only 4 canals of which 2 are situated almost at midline with one below and the fourth, not always clearly seen, dorsal to the other three. The selvage is distinct around the anterior and ventral margins.

### *Dimensions*

HOLOTYPE. Io. 551 female carapace (Pl. 5, figs. 7-10), length 0.80 mm.; height 0.53 mm.; width 0.57 mm.

### PARATYPES

Io. 552 male carapace (Pl. 6, figs. 1, 2, 5, 6), length 0.92 mm.; height 0.59 mm.; width 0.63 mm.

Io. 553 female carapace (Pl. 6, figs. 3, 4, 7, 9), length 0.83 mm.; height 0.55 mm.; width 0.55 mm.

Io. 554 left valve female (Pl. 7, fig. 2; text-fig. 7), length 0.70 mm.; height 0.55 mm. (broken).

Io. 555 carapace (Pl. 7, fig. 1; text-fig. 6), length 0.60 mm.; height 0.39 mm.; width 0.39 mm.

Io. 556 left valve female (Pl. 6, figs. 8, 10; Pl. 7, fig. 3), length 0.72 mm.; height 0.48 mm.

Io. 557 right valve (Pl. 7, fig. 4), length 0.57 mm.; height 0.39 mm.



REMARKS. Ostracod I of Apostolescu (1959, pl. 4, figs. 67, 68) resembles this species very closely and is most probably congeneric. *Pneumatocythere bajociana* is common throughout the Lincolnshire Limestone, but, because of its poor preservation there an accurate description of the genus and species was dependent upon better material obtained from the Yons Nab Beds, which overlie the Millepore Oolite along the Yorkshire coast (see Bate, 1959) in the neighbourhood of Scarborough, and from the marl bed, underlying the Cave Oolite at South Cave.

### Genus **ACANTHOCY THERE** Sylvester-Bradley emend

EMENDED DIAGNOSIS. Shell subrectangular, convex in dorsal view surface more or less spiny with large, round, prominent eye tubercles. Hinge antimerodont or lobodont.

TYPE SPECIES. *Cythere sphaerulata* Jones & Sherborn, 1888.

REMARKS. The original diagnosis of the genus indicated a single type of dentition only, namely, lobodont. However, the presence of a species, within the Bajocian sediments, almost identical with *A. sphaerulata* (Jones & Sherborn) except for the possession of an antimerodont hinge, necessitates a revised diagnosis of the genus, and the erection of a new subgenus, *Protoacanthocythere*.

### Subgenus **PROTOACANTHOCY THERE** nov.

DIAGNOSIS. A subgenus of the genus *Acanthocythere* in which the hinge is antimerodont.

TYPE SPECIES. *Acanthocythere* (*Protoacanthocythere*) *faveolata* sp. nov.

### *Acanthocythere* (*Protoacanthocythere*) *faveolata* sp. nov.

(Pl. 7, figs. 5-13, Pl. 8, figs. 1-5)

DERIVATION OF NAME. Latin, *favus*, a honeycomb.

DIAGNOSIS. A species of *Protoacanthocythere* with honeycomb ornamentation in which spines are developed at the transects of individual pits and along marginal borders.

HOLOTYPE. Io 558, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 559-65 and Io. 815-20, horizon and locality as above.

DESCRIPTION. *Carapace* subrectangular to subquadrate in side view; sexual dimorphism apparent, the presumed males being the more elongate. Anterior broadly rounded, slightly oblique dorsally with a short anterodorsal slope terminating at a large, shiny, eye tubercle, situated just to one side of the anterior cardinal angle. Posterior evenly rounded in the left valve with a short slightly concave posterodorsal slope in the right valve. Dorsal margin straight, ventral margin concave anteromedially, convex posteromedially. Lateral posteroventral margin swollen, overhanging the ventral margin. A distinct, thickened marginal keel is developed around the anterior and posterior margins extending along the ventral



margin almost up to midpoint. Left valve slightly larger than the right, overlapping the right along the ventral and posterior margins, slightly at the anterior cardinal angle but practically not at all around the anterior and along the dorsal margin. Greatest length extends throughout midpoint, greatest height in the anterior third. Ornamentation consists of a reticulate honeycomb pattern of ridges. The development of spines over the surface is variable in each specimen, generally however, a spine is produced where one ridge transects another. Spines are also produced along ridges as conical shaped structures thickest at their base and varying in length. Ventrally there is greater tendency for the development of spines along each ridge. Some of the specimens are excessively spinose, others are almost without spines at all. *Normal pore canals*, large circular and few in number. *Hinge* antimerodont, consisting of terminal dentate ridges (with approximately 5 anterior and 5 posterior teeth) and a long, narrow, finely locellate median groove in the right valve; left valve with terminal loculate sockets and a median bar which appears smooth in the specimens examined due to wear. The antimerodont nature of the hinge being deduced from the left valve. No accommodation groove. *Muscle scars* consist of a subvertical, slightly crescentic row of 4 adductor scars with an anterodorsal antennal scar and an anteroventral mandibular scar. Anteriorly a well developed flange extends as far as the anterior cardinal angle, and is often spinose (Pl. 8, fig. 1). Posteriorly the flange is reduced although it extends dorsally as far as the posterior cardinal angle. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* few in number, straight and widely spaced around the anterior and posterior margins.

### Dimensions

HOLOTYPE. Io. 558 female carapace (Pl. 7, figs. 5-7), length 0.60 mm; height 0.35 mm.; width 0.27 mm.

### PARATYPES

Io. 559 male carapace (Pl. 7, figs. 10-13), length 0.65 mm.; height 0.37 mm.; width 0.36 mm.

Io. 560 left valve male (Pl. 8, fig. 2), length 0.64 mm.; height 0.39 mm.

Io. 561 right valve male (Pl. 7, figs. 8, 9), length 0.64 mm.; height 0.35 mm.

Io. 562 left valve female, length 0.61 mm.; height 0.37 mm.

Io. 563 right valve female (Pl. 8, fig. 1), length 0.61 mm.; height 0.37 mm.

Io. 564 right valve male (Pl. 8, figs. 3, 4), length 0.72 mm.; height 0.40 mm.

Io. 565 left valve male (Pl. 8, fig. 5), length 0.67 mm.; height 0.36 mm.

REMARKS. *Acanthocythere* (*Protoacanthocythere*) *faveolata* resembles *Acanthocythere sphaerulata* (Jones & Sherborn) in general shape, possession of prominent eye tubercles, similar radial pore canals and in the presence of dimorphism. The two species may, however, be distinguished by the possession of an antimerodont hinge and an obliquely rounded posterior in the former species. This ostracod occurs commonly throughout the Kirton Shale and the Kirton Cementstone Series of Lincolnshire.



Genus **FUHRBERGIELLA** Brand & Malz, 1962

Subgenus **PRAEFUHRBERGIELLA** Brand & Malz, 1962

**Fuhrbergiella (Praefuhrbergiella) arens** sp. nov.

(Pl. 8, figs. 6–15, Pl. 9, figs. 1–3)

DERIVATION OF NAME. Latin *arens*, dry or parched.

DIAGNOSIS. A species of the subgenus *Praefuhrbergiella* with distinctive ornamentation of irregular ridges giving the carapace a dried, shrivelled appearance. Particularly in the female dimorph the postero-ventrolateral border of the valves projects below the ventral surface. Hinge weakly entomodont.

HOLOTYPE. Io. 566, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 567–570 and Io. 821–22, horizon as above together with the Kirton Cementstone Series, Kirton Lindsey.

DESCRIPTION. *Carapace* subquadrate in outline, posteriorly flattened in dorsal view. Sexual dimorphism indicated by the more elongate dimorphs which are considered to be the males. In comparison with the more squat female dimorphs, the males are rare. Greatest length of carapace dorsal of midpoint in the female, extending through midpoint in the male. Greatest height in the anterior third. In dorsal view the sides of the carapace expand posteriorly in the female but are more uniformly convex in the male. As a result the greatest width is posterior in the female and median in the male. Dorsal margin straight with a slight dorsomedian convexity. Cardinal angles distinct. Ventral margin convex with a slight median incurvature. Anterior broadly and uniformly rounded, posterior triangular, more distinctly rounded in the male dimorph. Posterodorsal slope slightly concave, posteroventral slope convex. Anterior and posterior marginal areas flattened. Right valve in particular has a broad posterodorsal swelling which projects slightly above the dorsal margin. Ventrolateral border of both valves strongly convex, projecting below the ventral surface. In the male this swelling tends to be rather uniform along the length of the valve, whilst in the female it is more pronounced posteroventrally, giving the female carapace a triangular or deltoid appearance in dorsal view. Surface of carapace ornamented with an irregular pattern of thin platy ridges, ventrolaterally orientated parallel to the lateral border, elsewhere rather irregular but roughly anteroventral to posterodorsal, although minor ridges, horizontally directed, occur. The appearance afforded by the ridges is that of a shrivelled surface. An elongate eye swelling is situated at the anterior cardinal angle, below which is a rather deeply incised furrow opening at the dorsal margin and extending obliquely downwards and forwards for a short distance below the eye swelling. A deeply incised, crescent-shaped furrow, situated anteromedially on the carapace, marks the position of the adductor scars. Ventral surface flattened, ornamented by 4–5 longitudinal ridges on each valve, the outer two uniting close to the posterior. Left valve larger than right, overlapping it slightly along the ventral margin and around the anterior and posterior margins, and overreaching it dorsally. *Muscle scars* consist of a subvertical row of 4 small adductor scars with a rounded anterodorsal antennal scar and a small rounded anteroventral mandibular scar.



*Hinge* weakly entomodont, sufficiently developed in the anteromedian portion of the median element, particularly in the male dimorph, to be distinguished from an antimerodont hinge. Left valve with terminal loculate sockets and a median dentate bar, the latter in all cases too poorly preserved to confirm a more coarsely dentate anterior portion. No accommodation groove, although a narrow ledge is present above the median bar. In the right valve the hinge consists of terminal dentate ridges possessing 4-5 teeth, although generally there appears to be one tooth less anteriorly. Median groove loculate, expanded slightly in the anterior portion. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* simple, straight and rather widely spaced; anteriorly there are 7-8 pore canals whilst posteriorly there are approximately 4 in number of which 2 are situated medially and are slightly curved. The selvage is prominent around the free margin. A prominent flange extends around the anterior margin but becomes less well developed along the ventral margin.

### *Dimensions*

HOLOTYPE. Io. 566 female carapace (pl. 8, figs. 11, 12, 14, 15), length 0.53 mm.; height 0.32 mm.; width 0.32 mm.

### PARATYPES.

Io. 567 right valve male (Pl. 8, figs. 8, 10, 13), length 0.61 mm.; height 0.33 mm.

Io. 568 right valve female (Pl. 8, fig. 7; Pl. 9, figs. 1, 3), length 0.47 mm.; height 0.27 mm.

Io. 569 left valve female (Pl. 8, fig. 6; Pl. 9, fig. 2), length 0.48 mm.; height 0.30 mm.

Io. 570 right valve female (Pl. 8, fig. 9), length 0.48 mm.; height 0.28 mm.

REMARKS. *Fuhrbergiella* (*Praefuhrbergiella*) *arens* is similar to *Fuhrbergiella* (*P.*) *sauzei* Brand & Malz, to which it is probably ancestral. However, the present species differs from the latter (and other species described by Brand & Malz, 1962) in the possession of ridges rather more widely but less regularly spaced, and in the greater tendency of the posteroventral border of the female carapace to overhang the ventral margin. This species is common but not abundant in the type locality and in the Kirton Cementstone Series of Lincoln.

### Genus *AULACOCY THERE* nov.

DERIVATION OF NAME. Greek, *αὐλαξ*, -*akos*, a furrow, + *cythere*.

DIAGNOSIS. A genus of Progonocytherinae, rather subquadrate in outline with horse-shoe shaped swelling the opening of which is directed antroventrally. Left valve larger than right, projecting strongly above right valve in region of anterior cardinal angle. Eye swelling large, oval. Hinge antimerodont, without accommodation groove. Muscle scars a subvertical row of 4 adductor scars with rounded anterodorsal antennal scar and similarly shaped anteroventral mandibular scar. Radial pore canals few, straight and widely spaced.

TYPE SPECIES. *Aulacocythere punctata* sp. nov.



REMARKS. Two species of this genus have so far been found in the Middle Jurassic sediments of Lincolnshire, namely, *A. punctata* sp. nov. and *A. reticulata* sp. nov. Despite the variation in ornament as indicated by their specific names, both possess the horse-shoe shaped swelling, characteristic of the genus. Sexual dimorphism occurs in both species, the presumed males being more elongate in outline.

*Aulacocythere punctata* sp. nov.

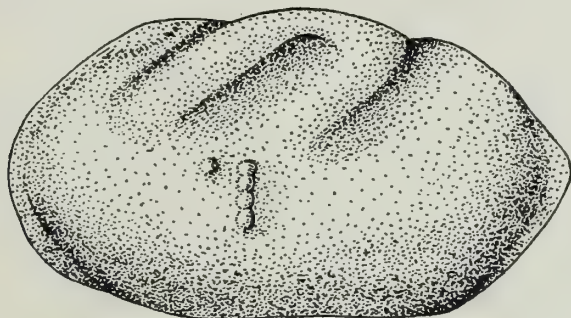
(Pl. 9, figs. 4-9, 11, 12, 14-15)

DERIVATION OF NAME. Latin, *punctum*, a small hole.

DIAGNOSIS. A species of *Aulacocythere*, with strongly punctate ornamentation.

HOLOTYPE. Io. 571, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 572-74 and Io. 823-28, horizon and locality as above.



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FIG. 14. *Aulacocythere* gen. nov. Left valve illustrating the generic characters: shape, horse-shoe swelling, eye swelling and muscle scars.

DESCRIPTION. *Carapace* somewhat inflated, subrectangular in side view. Sexual dimorphism apparent, the presumed males being more elongate: in dorsal view the males are also less inflated and tend to be parallel-sided. Dorsal margin in both valves straight. Cardinal angles in the left valve swollen, not so distinct in the right valve. Anterior uniformly rounded, slightly oblique dorsally in the right valve. Posterior narrowly rounded in the left valve, tapering in the right, becoming somewhat triangular with a short, concave, posterodorsal slope and a convex posteroventral slope. Left valve larger than the right, overreaching it on all sides, particularly anterodorsally, and also slightly overlapping it along the ventral margin. Anterior and posterior marginal areas compressed, distinct from the convex part of the valve. Shell surface ornamented by closely set puncta which cover the entire lateral part of the valve. Ventrally the carapace is less noticeably punctate and is here ornamented with 3-4 longitudinal ridges in each valve. The characteristic horse-shoe shaped swelling which opens anteroventrally, is particularly well developed. In both valves, but especially in the left, a distinct swelling below the anterior cardinal angle is indicative of an eye swelling. The ventrolateral border of the



carapace is strongly convex and overhangs the ventral surface, particularly in the posteroventral region. *Hinge* antimerodont? : left valve with terminal loculate sockets and a median bar rather worn in the specimens examined—no accommodation groove. Right valve with terminal dentate ridges possessing 7 teeth. Median groove poorly preserved may be locellate. *Muscle scars* which often appear as upraised spots on the exterior, consist of 4 oval adductor scars with a single, oval, anterodorsal antennal scar and a single, rounded, anteroventral mandibular scar. Selvage prominent around the free margin, outside of which there is a narrow flange. *Inner margin* and *line of concrescence* coincide, *radial pore canals* straight and widely spaced : approximately 10 anteriorly and 3-4 posteriorly.

### *Dimensions*

HOLOTYPE. Io. 571 male carapace (Pl. 9, figs. 8, 11, 14, 15) length 0.48 mm. ; height 0.27 mm. ; width 0.24 mm.

### PARATYPES.

Io. 572 right valve male (Pl. 9, figs. 4, 7) length 0.44 mm. ; height 0.24 mm.

Io. 573 right valve female (Pl. 9, fig. 5) length 0.40 mm. ; height 0.24 mm.

Io. 574 left valve female (Pl. 9, figs. 6, 12) length 0.41 mm. ; height 0.24 mm.

REMARKS. Although the antimerodont hinge can be clearly seen in *A. reticulata* it is difficult to state definitely whether this is so in *A. punctata*. In some respects this species resembles *Oligocythereis woodwardi* Sylvester-Bradley (1948, pl. 122, figs. 7-12) in general outline, but differs in the possession of a horse-shoe shaped swelling and an antimerodont? hinge. A common species occurring both in the Kirton Shale and the Kirton Cementstone Series of Lincolnshire.

### *Aulacocythere reticulata* sp. nov.

(Pl. 9, figs. 10, 13, 16-25 ; Pl. 10, fig. 1)

DERIVATION OF NAME. Latin, *reticulatus*, netlike.

DIAGNOSIS. A species of *Aulacocythere* with strong, reticulate ornamentation.

HOLOTYPE. Io. 575, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 576-79 and Io. 829-40, horizon and locality as above.

DESCRIPTION. *Carapace* subrectangular in outline ; sexual dimorphism apparent, presumed males being more elongate. Shell surface ornamented with a strong reticulate net work of 5 or 6 sided pits. The horse-shoe swelling prominent in the type species, is also prominent here. Eye swelling large, oval, situated just below the anterior cardinal angle. Valves convex, although males, as seen in dorsal view, tend to be rather parallel-sided. Ventrolateral border slightly swollen ; anterior broadly rounded ; posterior narrowly rounded, acuminate-triangular in the right valve. Dorsal margin straight, convex anteriorly and posteriorly in the left valve ; ventral margin slightly concave medially. Ventral surface of each valve ornamented with 3-4 longitudinal ridges. Anterior and posterior margins compressed, forming



a marginal border. Left valve larger than the right which it overreaches on all sides, particularly in the region of the anterior cardinal angle. Greatest length median, greatest height in the anterior third, greatest width in the posterior half. *Hinge* antimerodont; left valve with terminal loculate sockets and a coarsely denticulate median bar, no accommodation groove. In the right valve the hinge consists of terminal dentate ridges bearing 6 teeth and a locellate groove. Selvage prominent around the free margin, outside of which there is a distinct flange. *Radial pore canals* straight, few in number (exact number not observed) and widely spaced. *Muscle scars*, which are often seen on the exterior as upraised spots, as for the genus. *Inner margin* and *line of concrescence* coincide. Young instars possess a left valve which strongly projects above the right valve dorsally.

### *Dimensions*

HOLOTYPE. Io. 575 female carapace (Pl. 9, figs. 10, 13, 20, 21), length 0.44 mm; height 0.29 mm; width 0.27 mm.

### PARATYPES.

Io. 576 male carapace (Pl. 9, figs. 16-19), length 0.49 mm.; height 0.25 mm.; width 0.27 mm.

Io. 577 left valve male (Pl. 10, fig. 1), length 0.49 mm.; height 0.28 mm.

Io. 578 juv. carapace (Pl. 9, figs. 23, 24), length 0.36 mm.; height 0.20 mm.; width 0.18 mm.

Io. 579 right valve male (Pl. 9, figs. 22, 25), length 0.52 mm.; height 0.27 mm.

REMARKS. A species so far recorded only from the type locality in Lincolnshire where it occurs fairly frequently throughout the entire thickness of the Kirton Shale.

### Genus *CAMPTOCYTHERE* Triebel, 1950

REMARKS. *Camptocythere* is placed in the Progonocytherinae on the evidence of the muscle scars and radial pore canals.

TYPE SPECIES. *Camptocythere praecox* Triebel, 1950.

### *Camptocythere lincolnensis* sp. nov.

(Pl. 10, figs. 2-13)

DIAGNOSIS. A species of *Camptocythere* with distinct quadrate outline and ornament of rather large irregular pits.

HOLOTYPE. Io. 580, Kirton Cementstone Series, Greetwell Quarry, Lincoln.

PARATYPES. Io. 581-83, horizon and locality as above.

DESCRIPTION. *Carapace* quadrate, rather angular in outline with a broad, flattened area in the dorsomedian part of the carapace. Shell surface ornamented with large, irregularly shaped pits. Sexual dimorphism suggested by the presence



of a single left valve slightly more elongate than the other left valves examined, but the evidence is not strong. Greatest length of carapace along midline, greatest height in the anterior third. Greatest width situated in the posterior third, although in dorsal view the carapace is virtually parallel-sided with a slight compression medially. Anteriorly and posteriorly there is a narrow, compressed marginal border. *Left valve* slightly larger than the right which it overlaps along the ventral margin and overreaches around the anterior and posterior margins; dorsally the right valve overlaps the left. In outline the left valve tends to be subquadrate with a straight dorsal margin, the latter projecting dorsally at the anterior cardinal angle. Posterior cardinal angle broadly rounded. Anterior broadly and uniformly rounded. Posterior tapering, narrowly rounded. Ventral margin strongly convex, sweeping upwards posteriorly. *Right valve* quadrate in outline with a very slightly convex dorsal margin, sloping gently to the posterior. Cardinal angles more sharply angled than in the left valve. Anterodorsal slope short and slightly convex, posterodorsal slope short and slightly concave. Anterior margin rounded, posterior broadly triangular. Ventral margin broadly convex with a median incurvature. In both valves the ventrolateral border is swollen, overhanging the ventral surface. Left valve swollen in the region of the anterior cardinal angle and to a lesser degree along the dorsal margin. The right valve is equally swollen at the anterior and posterior angles, but to a lesser degree dorsomedially. The median depression in both valves is separated from the dorsal margin by the dorsal swelling. *Hinge* lopodont. In the right valve the terminal hinge elements are non-dentate, and connected by a long, straight, smooth median groove. In the left valve the terminal sockets are smooth, open to the interior of the valve ventrally. The smooth median element in the left valve is formed by the slightly downset dorsal edge of the valve. No accommodation groove. *Muscle scars* consist of a subvertical row of 4 rounded adductor scars with a rather oval anterodorsal antennal scar, no mandibular scar has been seen. *Radial pore canals* straight, widely spaced, approximately 8-10 anteriorly and 2-3 posteriorly. *Inner margin* and *line of concrescence* coincide. The selvage is prominent around the free margin in both valves.

### *Dimensions*

HOLOTYPE. Io. 580 carapace (Pl. 10, figs. 2-5), length 0.48 mm.; height 0.31 mm.; width 0.28 mm.

### PARATYPES.

Io. 581 left valve (Pl. 10, figs. 8, 9), length 0.47 mm.; height 0.32 mm.

Io. 582 right valve (Pl. 10, figs. 11, 12), length (broken) 0.44 mm.; height 0.29 mm.

Io. 583 right valve (Pl. 10, figs. 6, 7, 10, 13), length 0.44 mm.; height 0.29 mm.

REMARKS. *Camptocythere lincolnensis* differs from other species of the genus in that the right valve does not project so strongly above the left and the hinge does not slope so strongly to the posterior. This is a rather rare ostracod, so far only found in the Kirton Cementstone Series.



Subfamily **PLEUROCYTHERINAE** Mandelstam, 1960

REMARKS. This subfamily, introduced by Mandelstam (1960) was included by Howe (Moore, 1961 : Q. 327) in the subfamily Protocytherinae Ljubimova (1955.) However it is considered to be a satisfactory group for those ostracods which have the following characters in common. Carapace elongate, often strongly ornamented. Hinge variable. Inner margin and line of concrescence coincide, the duplicature being of moderate width. Radial pore canals curved. Muscle scars consisting of a subvertical row of 4 adductor scars with a kidney-shaped anterodorsal antennal scar and an oval or rounded anteroventral mandibular scar (type A). At the moment only *Pleurocythere* Triebel (1951) is included in the subfamily.

Genus **PLEUROCYTHERE** Triebel, 1951

*Pleurocythere kirtonensis* sp. nov.

(Pl. 10, figs. 14-18, Pl. 11, figs. 1-5)

DIAGNOSIS. A species of *Pleurocythere* with three well developed longitudinal ridges and prominent anterior marginal ridge, the latter not connected to median longitudinal ridge. Carapace strongly reticulate.

HOLOTYPE. Io. 584, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 585-87 and Io. 841-46, horizon and locality as above.

DESCRIPTION. *Carapace* elongate, rounded anteriorly, acuminate-triangular posteriorly. Dorsal margin straight to slightly concave, in the right valve, with a slight inclination to the posterior, convex in the left. Apart from the dorsal keel of the left valve the ornamentation of the carapace is the same for both valves. The anterior marginal ridge is a continuation of the oblique anterodorsal ridge. Of the three longitudinal ridges, the two situated on the ventrolateral border are the most strongly developed. The oblique median ridge (uppermost of the three) is short in this species, to the rear of which is a short posterodorsal ridge, typical of the genus. This latter ridge is most strongly developed in the right valve. Shell surface rather coarsely reticulate. A slight swelling at the termination of the oblique anterodorsal ridge is suggestive of an eye swelling. Left valve larger than the right which it overlaps midventrally and overreaches dorsally. *Hinge* merodont, consisting in the left valve of terminal loculate sockets and a median bar, above which is a shallow accommodation groove. In the right valve the terminal elements bear 5 teeth both anteriorly and posteriorly. Median groove poorly preserved. It is therefore difficult to determine whether the hinge is antimerodont or hemimerodont. *Muscle scars* not seen. *Inner margin and line of concrescence* coincide, *radial pore canals* are long anteriorly although not clearly seen. Posteriorly the radial canals, which are 4 in number, curve slightly outwards away from midline. A well developed flange is present outside the selvage, being particularly well developed around the anterior margin, often poorly represented ventrally, especially in the left valve.

### *Dimensions*

HOLOTYPE. Io. 584 female carapace (Pl. 10, figs. 14, 16, Pl. 11, figs. 4, 5), length 0.68 mm. ; height 0.37 mm. ; width 0.31 mm.



## PARATYPES.

- Io. 585 left valve female (Pl. 10, figs. 15, 17), length 0.67 mm. ; height 0.35 mm.  
 Io. 586 right valve male (Pl. 10, fig. 18 ; Pl. 11, figs. 2, 3), length 0.68 mm. ; height 0.33 mm.  
 Io. 587 right valve male (Pl. 11, fig. 1), length 0.73 mm. ; height 0.36 mm.

REMARKS. *Pleurocythere kirtonensis* resembles *P. impar* Triebel (1951, pl. 45, figs. 8-12) from which it can be distinguished by the absence of a connecting ridge between the median ridge and the anterodorsal part of the marginal ridge. It is a common species within the Kirton Shale and also in the Kirton Cementstone Series of Kirton Lindsey.

***Pleurocythere nodosa* sp. nov.**

(Pl. 11, figs. 6-21)

DERIVATION OF NAME. Latin, *nodosus*, knotted.

DIAGNOSIS. A species of *Pleurocythere* with two longitudinal ridges, poorly developed oblique anterior ridge and large eye swelling. Small, rounded nodes ornament the shell surface. Anterior and posterior margins dentate.

HOLOTYPE. Io. 588, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 589-92 and Io. 847-55, horizon and locality as above.

DESCRIPTION. *Carapace* elongate-quadrate, rounded anteriorly. Posterior acuminate-triangular. Both the anterior and posterior margins are dentate. Sexual dimorphism indicated by the presence of elongate specimens which are considered to be the males. Greatest length median, greatest height and width in the anterior third. Left valve larger than the right which it overlaps along the ventral margin. Dorsal keel in the left valve and a curved posterodorsal ridge in the right valve ; otherwise the ornamentation of both valves is the same. Only two longitudinal ridges occur in this species, a horizontal ventrolateral and an oblique median ridge, the latter giving off an anteriorly directed ridge from its posterior part, in the right valve. Shell surface smooth except for small nodes, irregularly scattered between the ridges. A distinct eye swelling is developed just below the anterior cardinal angle. Eye swelling connected in young instars to a thin, anterior ridge, poorly developed, if at all, in adults. Ventral surface with three faint ridges on each valve. *Hinge* antimerodont. Left valve with terminal loculate sockets and a finely denticulate median bar, no accommodation groove. Right valve with terminal dentate ridges (possessing approximately 7 teeth) and a long, narrow locellate median groove, although the latter is not clearly seen because of the state of preservation. *Inner margin* and *line of concrescence* coincide, radial pore canals long, but not clearly seen. *Muscle scars* not seen. A flange extends around the anterior and posterior margins outside the selvage, but ventrally it is only poorly developed.

*Dimensions*

HOLOTYPE. Io. 588 female carapace (Pl. 11, figs. 6, 7, 9, 10), length 0.47 mm. ; height 0.25 mm. ; width 0.23 mm.



## PARATYPES.

Io. 589 male carapace (Pl. 11, figs. 13-16), length 0.49 mm.; height 0.24 mm.; width 0.20 mm.

Io. 590 right valve male (Pl. 11, figs. 12, 17), length 0.49 mm.; height 0.23 mm.

Io. 591 left valve female (Pl. 11, figs. 8, 11), length 0.47 mm.; height 0.25 mm.

Io. 592 juv. carapace (Pl. 11, figs. 18-21), length 0.36 mm.; height 0.17 mm.; width 0.16 mm.

REMARKS. This species differs from *P. kirtonensis* in the possession of a surface ornament of small nodes, large eye swelling and the attachment of the posterodorsal ridge to the posterior part of the median ridge. Although found with *P. kirtonensis*, in the Kirton Shale, this smaller species is not nearly as common.

## Family CYTHERIDEIDAE Sars, 1925

## Subfamily CYTHERIDEINAE Sars, 1925

Genus *DOLOCY THERE* Mertens, 1956

1959. *Lophodentina*, Apostolescu, p. 813.

DIAGNOSIS. A thick-shelled subrectangular genus of Cytherideinae possessing 8-12, straight, anterior and about 6 posterior radial pore canals. Hinge lophodont. Shell surface variously ornamented. Left valve larger than right.

TYPE SPECIES. *Dolocythère rara* Mertens, 1956.

REMARKS. On the general characters of shape, thickness of the carapace, simple radial pore canals associated with a moderately developed duplicature in which the inner margin and line of concrescence coincide, *Dolocythère* Mertens 1956 has been placed in the family Cytherideidae Sars 1925, subfamily Cytherideinae Sars 1925. The type of muscle scar arrangement with a bill-hook shaped antennal scar and a mandibular support spot, is considered here to be typical of the family.

*Dolocythère maculosa* sp. nov.

(Pl. 12, figs. 1-11; Text-figs. 8, 9)

DERIVATION OF NAME. Latin, *maculosus*, spotted.

DIAGNOSIS. A species of *Dolocythère*, slightly constricted in mid-dorsal/mid-ventral region and ornamented with large, circular pits irregularly scattered over carapace.

HOLOTYPE. Io. 609, marl below the Cave Oolite, Eastfield Quarry, South Cave, Yorkshire.

PARATYPES. Io. 610-13 and Io. 856-75, horizon and locality as above.

DESCRIPTION. *Carapace* subrectangular in side view, dorsal and ventral margins slightly concave medially, anterior uniformly rounded, posterior obliquely rounded. Greatest width of carapace posteroventral, greatest length passing through midpoint,



greatest height in the anterior third. Left valve slightly larger than the right which it overreaches around the anterior margin, slightly around the posterior margin, and with some overlap at about the centre of the ventral margin. Surface of carapace covered with large, circular, rather shallow pits, within each of which is a large normal pore canal. Anteriorly and posteriorly the marginal border is compressed, partially obscured posteroventrally by the convexity of the carapace. Cardinal angles distinct, slightly swollen in dorsal view. *Hinge* lophodont. Left valve with the smooth median element formed by the dorsal edge of the valve which is here slightly downset; the terminal sockets, produced by the upward projection of the dorsal margin remain open ventrally. In the right valve the smooth terminal elements, extensions of the selvage, are bent at the cardinal angles, whilst medially there is a long, straight, narrow groove above which there is a long narrow bar, the latter separated from the dorsal edge of the valve by a faint groove. *Inner margin* and *line of concrescence* coincide. *Radial pore canals* straight and widely spaced, 9-10 anteriorly, 3 posteriorly. The *muscle scars* consist of a subvertical row of 4 adductor scars, the two central scars being the more elongate. The antennal scar, situated anterodorsally, is composed of two distinct scars, a large, bill-hook shaped scar and a smaller scar situated above the lower limb of the bill-hook. The opening of the antennal scar is directed obliquely upwards towards the anterior cardinal angle. In some specimens (Pl. 12, fig. 7) an oval "mandibular stutzfleck" (mandibular support spot) can be seen situated in front of the dorsal adductor scar. The large, oval mandibular scar is situated anteroventrally to the adductor scars. In both valves the selvage is prominent around the free margin, external to which is a well developed flange, the latter extending around the anterior, posterior and ventral margins of the right valve but largely confined to the anterior margin of the left valve.

### *Dimensions*

HOLOTYPE. Io. 609 left valve (Pl. 12, figs. 1, 2, 6), length 0.60 mm.; height 0.35 mm.

### PARATYPES.

Io. 610 carapace (Pl. 12, figs. 8, 9), length 0.64 mm.; height 0.35 mm.; width 0.33 mm.

Io. 611 right valve (Pl. 12, figs. 3-5), length 0.61 mm.; height 0.37 mm.

Io. 612 left valve (Pl. 12, figs. 10, 11, Text-fig. 8), length 0.62 mm.; height 0.36 mm.

Io. 613 right valve (Pl. 12, fig. 7, Text-fig. 9), length 0.60 mm.; height 0.35 mm.

REMARKS. *Dolocythère maculosa* can be distinguished from *D. rara* Mertens (1956, pl. 10, figs. 33-37) and *Lophodentina lacunosa* Apostolescu (1959, pl. 3, figs. 56, 57) by its lack of a reticulate ornament. The specimens of *D. maculosa* described here were obtained from the marl below the Cave Oolite of South Yorkshire, where they are extremely common. Although common also in the Kirton Shale and Kirton Cementstone Series of Lincolnshire the specimens are too poorly preserved for accurate description.



Family **SCHULERIDEIDAE** Mandelstam 1959Subfamily **SCHULERIDEINAE** Mandelstam 1959

REMARKS. Four genera (*Schuleridea* Swartz & Swain, 1946, *Asciocythere* Swain, 1952, *Galliaecytheridea* Oertli, 1957, and *Nodophthalmocythere* Malz, 1958) placed in the family Cytherideidae Sars, 1925, subfamily Cytherideinae Sars, 1925, in the *Invertebrate Paleontology Treatise, Part Q*, are closely related in shape, radial pore canals and arrangement of the muscle scars (Type "C"). A fifth genus, *Praeschuleridea* gen. nov., is also closely related in these three characters. All these genera differ from the others placed within the Cytherideinae in the arrangement of the muscle scars, to some extent in outline and in the tendency for the radial pore canals to be arranged fan-like around the anterior margin. Indeed, there appears to be little reason to retain these genera within the family. Hence the subfamily Schulerideinae Mandelstam (1959) is retained and the Schulerideidae Mandelstam given family status.

The genera placed in the subfamily *Cuneocytherinae* Mandelstam, 1960 (Moore, 1961) also belong in this family.

Genus **PRAESCHULERIDEA** nov.

DERIVATION OF NAME. Latin, *prae* before, + *Schuleridea* (an ostracod genus erected by Swartz & Swain, 1946).

DIAGNOSIS. Carapace ovoid in outline, ornamented or smooth. Hinge paleohemimerodont. Greatest length of carapace along midlength. Radial pore canals arranged in a fan, curving slightly outwards away from a line drawn through midpoint, 12-16 anteriorly, 4-6 posteriorly. Muscle scars consist of a crescentic row of 4 oval adductor scars with centrally situated anterior antennal scar, often kidney-shaped with small secondary scar in front but sometimes rounded: mandibular scar, when seen, in front of and below adductor scars.

TYPE SPECIES. *Cytheridea subtrigona* Jones & Sherborn, 1888.

REMARKS. *Praeschuleridea* differs from *Schuleridea* Swartz & Swain in having a more uniformly ovoid outline in lateral view, the greatest length being through midpoint and not ventral of midpoint as is often the case in the latter genus. Radial pore canals are identical in both genera except in number—there are about 30 anterior and 10 posterior in *Schuleridea* and only 12-16 anterior and 4-6 posterior in *Praeschuleridea*. Finally, whereas the hinge in *Schuleridea* is paleomerodont, with the median element of the right valve projecting beyond the commissure in dorsal view, the hinge in *Praeschuleridea* is paleohemimerodont, with the median element of the left valve projecting beyond the commissure as seen in dorsal view.

***Praeschuleridea subtrigona*** (Jones & Sherborn)

(Pl. 12, figs. 12-16; Pl. 13, figs. 1-9; Text-fig. 15)

1888 *Cytheridea subtrigona* Jones & Sherborn, p. 265, pl. 2, fig. 9a-c.

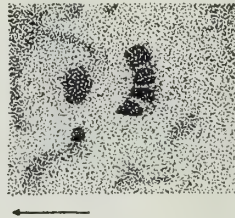
DIAGNOSIS. A species of *Praeschuleridea* with subtrigonal carapace when viewed



laterally. Right valve more elongate than left, more acuminate posteriorly. Hinge paleohemimerodont. Muscle scars and radial pore canals as for genus. Carapace smooth with very fine puncta.

LECTOTYPE (chosen here) I. 1838, a single right valve, Blue Fuller's Earth Clay, Midford, Bath.

DESCRIPTION. *Carapace* oval-subtriangular in side view, strongly convex with greatest width just behind valve centre. Sexual dimorphism strongly pronounced, the presumed males being the more elongate. Surface of valves finely punctate but may appear smooth and devoid of puncta if poorly preserved. A narrow, anterior marginal border on each valve. Left valve larger than the right which it overreaches on all sides, but more strongly along the dorsal and ventral margins, and which it strongly overlaps midventrally. Greatest length for both valves lies along midlength. Greatest height in the left valve at valve centre, but in the right valve in front of centre. As the right valve is more elongate than the left, and as the latter is subtrigonal, the dorsal margin of the left valve is more broadly convex than



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FIG. 15. Muscle scars, *Praeschuleridea subtrigona* (Jones & Sherborn). Io. 594.  $\times 200$

that of the right valve, and the cardinal angles are more strongly distinct in the latter. Anterior broadly rounded in both valves, posterior acuminate, more so in the right than in the left. The ventrolateral border in both valves slightly overhangs the ventral surface medially. A small swelling with an oblique furrow below is situated just beneath the anterior cardinal angle in the right valve—this feature, which may represent an eye swelling, is not seen in the left valve. *Hinge* paleohemimerodont. Left valve with terminal loculate sockets united across an upraised median bar by a long, narrow, smooth groove: above the median element a broad accommodation groove is developed. In the right valve the terminal dentate ridges bear 5 teeth anteriorly and 6–7 teeth posteriorly: a long, slender, smooth median bar fits into the groove of the left valve, but is itself situated in a depressed, groove-like depression and does not project beyond the line of the commissure when viewed dorsally. *Inner margin* and *line of concrescence* coincide to form a fairly broad duplicature. *Radial pore canals* splayed into a fan, approximately 12–16 anteriorly (11 seen in a juvenile specimen) and 4–6 posteriorly. *Muscle scars* consist of a crescentic row of 4 oval adductor scars with a single, rounded, anteromedian antennal scar. The mandibular scar is situated anteroventrally relative to the adductor scars.



*Dimensions*

Io. 593 left valve female (Pl. 13, fig. 6), length 0.51 mm. ; height 0.35 mm.

Io. 594 right valve female (Pl. 13, fig. 4 ; Text-fig. 15), length 0.47 mm. ; height 0.28 mm.

Io. 595 left valve female (Pl. 12, fig. 16), length 0.56 mm. ; height 0.35 mm.

Io. 596 male carapace (Pl. 13, figs. 1-3), length 0.53 mm. ; height 0.35 mm. ; width 0.27 mm.

Io. 597 female carapace (Pl. 12, figs. 12-15), length 0.51 mm. ; height 0.35 mm. ; width 0.27 mm.

Io. 598 right valve male (Pl. 13, figs. 7, 9), length 0.51 mm. ; height 0.29 mm.

Io. 599 left valve female (Pl. 13, figs. 5, 8), length 0.53 mm. ; height 0.36 mm.

REMARKS. Apart from the recorded occurrence of this species by Jones & Sherborn (1888), *P. subtrigona* is abundant in the middle Bajocian, Kirton Shale, Kirton Lindsey, and throughout the Lower Lincolnshire Limestone of Lincolnshire.

## Family PROTOCYTHERIDAE Ljubimova 1955

REMARKS. The subfamily Protocytherinae Ljubimova, 1955, is placed as a subfamily of the Progonocytheridae Sylvester-Bradley, 1948, in the *Treatise on Invertebrate Paleontology* (Moore, 1961 : Q327). As mentioned previously (p. 191) the subfamily has been removed from the Progonocytheridae on the grounds that it did not belong there and resulted in the establishment of a strictly artificial family. The subfamily Protocytherinae is here raised to the level of a family, an important feature of which is the U- or V-shaped antennal muscle scar.

## Subfamily KIRTONELLINAE nov.

DIAGNOSIS. Subquadrate, elongate to piriform with ventrolateral border often tending to overlap ventral margin. Hinge variable with or without accommodation groove. Duplicature of medium development with inner margin and line of concrescence coinciding. Radial pore canals straight, few and widely spaced. Adductor muscle scars consist of a subvertical row of 4 scars with anterodorsal U- or V-shaped antennal scar and anteroventral, rounded mandibular scar. Left valve larger than right. Shell surface smooth or ornamented.

REMARKS. This subfamily is differentiated from the Protocytherinae by the possession of straight radial pore canals, simple in character and few in number.

Genus *KIRTONELLA* nov.

DERIVATION OF NAME. After type locality.

DIAGNOSIS. A genus of the Kirtonellinae, dimorphic, subtriangular to subquadrate in outline with ventrolateral border of carapace tending to project ventrally as an



overfold. Hinge antimerodont. An eye swelling may be present just below anterior cardinal angle.

TYPE SPECIES. *Kirtonella plicata* sp. nov.

REMARKS. Although there is some resemblance between the female dimorphs of the type species of this genus and *Procytheridea* Peterson, the former can be distinguished by the type of overfold of the ventrolateral border and the presence of a U-shaped antennal muscle scar. There is no resemblance between the more elongate, male dimorphs of the respective type species. The dorsal margin, which is rather steeply angled in *Procytheridea* (the posterior cardinal angle being broad and indistinct), is less steeply inclined in *Kirtonella*, where the posterior cardinal angle is prominent.

***Kirtonella plicata* sp. nov.**

(Pl. 13, figs. 10-19; Pl. 14, figs. 1-6, 11, 12; Text-fig. 12)

DERIVATION OF NAME. Latin, *plicatus*, folded.

DIAGNOSIS. A species of *Kirtonella* with strong parallel folds extending along ventrolateral margin. Remainder of carapace ornamented with weak transverse wrinkles and pits.

HOLOTYPE. Io. 600, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 601-08 and Io. 879-81, horizon and locality as above.

DESCRIPTION. *Carapace* subquadrate to subtriangular in outline. Sexual dimorphism strongly apparent, the presumed males being the more elongate, the females shorter and subtriangular. In the latter, the dorsal margin is rather more strongly arched than in the male, where the dorsal margin is straight, being only slightly arched posteriorly. The downward slope of the dorsal margin and the upward slope of the ventral margin are responsible for the characteristic outline of the female dimorph. In the male the posterior taper is limited to the posterior third, dorsal and ventral margins being roughly parallel elsewhere. Anterior in both sexes broadly rounded, posterior triangular. Ventral margin slightly convex, sloping upwards posteriorly in the female. In both sexes the ventral incurvature of the carapace is situated just anterior of the valve middle. Left valve larger than the right, which it overlaps slightly along the ventral margin, elsewhere the left valve overreaches the right. A shallow groove extends around the anterior margin producing a raised outer rim. In side view a ventrolateral overfold of the valve, which tends to be more strongly developed posterolaterally, is ornamented by 3 longitudinal ridges, with occasionally 2 further rather faint ridges dorsal to these. Ventral surface of each valve ornamented by 3 or 4 longitudinal ridges. Shell surface ornamented laterally by strong circular pits, which tend to become irregular in shape in some specimens, often increasing in size medially where weak transverse ridges are developed. A shallow sulcus is situated just behind the position of the adductor muscle scars. Greatest length of carapace extends through midpoint whilst the greatest height is at the anterior cardinal angle. Greatest width just behind and above midpoint, particularly so in the case of the male dimorph which develops a distinct posterodorsal bulge. A slight swelling, particularly noticeable



in the left valve, may be seen below the anterior cardinal angle and probably represents an eye swelling. Hinge antimerodont, with, in the left valve, terminal loculate sockets and a coarsely dentate median bar, above which there is a narrow accommodation groove: in the right valve the hinge consists of 6 anterior and 7 posterior teeth separated by a loculate median groove. The *muscle scars* consist of a subvertical row of 4 rounded adductor scars with a U-shaped anterodorsal antennal scar and a circular anteroventral mandibular scar. *Line of concrescence* and *inner margin* coincide, producing a broad duplicature. *Radial pore canals* long, straight and widely spaced around the anterior margin, where there may be approximately 11 in number; posteriorly there are 4 radial canals. Selvage prominent, outside of which a flange is developed around the anterior margin and along the anterior two-thirds of the ventral margin.

### *Dimensions*

HOLOTYPE. Io. 600 female carapace (Pl. 13, figs. 10-13), length 0.51 mm.; height 0.31 mm.; width 0.27 mm.

### PARATYPES.

Io. 601 right valve male (Pl. 14, fig. 12), length 0.64 mm.; height 0.32 mm.

Io. 602 left valve male (Pl. 13, fig. 19; Pl. 14, figs. 3, 11), length 0.64 mm.; height 0.33 mm.

Io. 603 right valve male (Pl. 13, fig. 16), length 0.71 mm.; height 0.36 mm.

Io. 604 male carapace (Pl. 14, figs. 1, 2), length 0.67 mm.; height 0.35 mm.; width 0.30 mm.

Io. 605 left valve female (Pl. 13, figs. 17, 18; Pl. 14, fig. 5), length 0.43 mm.; height 0.25 mm.

Io. 606 right valve female (Pl. 14, figs. 4, 6), length 0.52 mm.; height 0.30 mm.

Io. 607 left valve female (Pl. 13, fig. 15), length 0.56 mm.; height 0.35 mm.

Io. 608 left valve female (Pl. 13, fig. 14; Text-fig. 12), length 0.56 mm.; height 0.33 mm.

REMARKS. In addition to the type locality *K. plicata* is also present in the marly bed (*A. crossi* Bed ?) at the top of the Kirton Cementstone Series, Greetwell Quarry, Lincoln.

### Genus **SYSTEMOCYTHERE** nov.

DERIVATION OF NAME. Greek, *σύστημα*, tapering to a point, + *cythere*.

DIAGNOSIS. Kirtonellinae, elongate to oval-subquadrate, tapering strongly to posterior, particularly in male dimorph. Right valve strongly overlapped by left in region of cardinal angles. Hinge antimerodont.

REMARKS. *Systemocythere* differs from *Kirtonella* gen. nov., in possessing a much more strongly tapered carapace and in the type of valvular overlap.

TYPE SPECIES. *Systemocythere exilofasciata* sp. nov.



*Systemocythere exilofasciata* sp. nov.

(Pl. 14, figs. 7-10, 13-17; Pl. 15, figs. 1-4)

DERIVATION OF NAME. Latin, *exilis*, poor; *fasciatus*, banded.

DIAGNOSIS. A species of *Systemocythere* with ornamentation of longitudinal ridges weakly developed in posterolateral region of carapace; elsewhere shell surface tends to be smooth.

HOLOTYPE. Io. 614, Kirton Cementstone Series, Kirton Cement Quarry, Kirton Lindsey.

PARATYPES. Io. 615-19, Io. 628, Io. 876-78, horizon and locality as above and from Cave Oolite and marl beneath, Eastfield Quarry, South Cave.

DESCRIPTION. Carapace strongly dimorphic, the female rather subquadrate with a short, tapered posterior; the male much more elongate, the posterior being drawn out and acuminate. Greatest length in both sexes extends below midpoint, greatest height in the anterior third, closer to midpoint in the male. Greatest width in the posterior third. Dorsal margin straight, sloping to the posterior at about 45 degrees. Anterior cardinal angle well rounded, almost "umbonate"; posterior cardinal angle distinct, particularly in the left valve. Anterodorsal slope slightly convex, much longer in the male. Posterodorsal slope slightly concave. Ventral margin convex, incurved anteromedially. Anterior margin obliquely rounded, posterior narrowly rounded, acuminate in the male, broadly triangular in the female. The posteroventral part of the carapace in both dimorphs is noticeably swollen with the lateral border slightly overhanging the ventral surface. *Normal pore canals* round and widely scattered over the shell surface. Ornamentation weak, with longitudinal ridges in the posterolateral region, the ridges following the ventral outline of the carapace. Secondary, weak, obliquely transverse ridges may be present in the posterior part of the carapace, but their presence, as in the case of the longitudinal ridges, is dependent on the state of preservation of the specimen. The ventral surface of the carapace is strongly ornamented by 4 longitudinal ridges on each valve. Left valve larger than the right which it strongly overlaps along the ventral margin (the degree of overlap increasing towards the posterior), and which it also strongly overlaps in the region of the cardinal angles; at the extreme anterior the valves meet without overlap whilst posteriorly the left valve overreaches the right. Along the dorsal margin the valves are withdrawn, almost exposing the median part of the hinge. *Hinge* strongly antimerodont. Left valve with loculate terminal sockets and a coarsely dentate median bar, above which is an elongate accommodation groove. Right valve with terminal dentate ridges bearing from 5-6 teeth and a coarsely loculate median groove. *Muscle scars* consist of a subvertical row of 4 adductor scars, of which the middle two are laterally elongate whilst the dorsal adductor scar is often elongate dorso-ventrally. The ventral adductor scar is oval, but in a single specimen it was seen to be divided into two small scars. The antennal scar is situated anterodorsally and is broadly U-shaped, formed by the fusion of 2 or more scars. The antero-



ventral, oval mandibular scar is not often seen. *Inner margin* and *line of concretion* coincide. *Radial pore canals* long, straight and widely spaced, approximately 10-11 anteriorly and about 4 posteriorly.

### *Dimensions*

HOLOTYPE. Io. 614 female carapace (Pl. 14, figs. 7-10), length 0.57 mm. ; height 0.33 mm. ; width 0.35 mm.

### PARATYPES.

Io. 615 male carapace (Pl. 14, figs. 14, 15), length 0.63 mm. ; height 0.33 mm. ; width 0.36 mm.

Io. 616 right valve male (Pl. 14, fig. 17), length 0.61 mm. ; height 0.32 mm.

Io. 617 female carapace, length 0.60 mm. ; height 0.37 mm. ; width 0.37 mm.

Io. 618 left valve male (Pl. 14, figs. 13, 16 ; Pl. 15, fig. 3), length 0.71 mm. ; height 0.41 mm.

Io. 619 right valve male (Pl. 15, figs. 1, 2, 4), length 0.67 mm. ; height 0.37 mm.

REMARKS. The ratio of males to females in this species is an interesting one. In the type horizon, no male dimorphs have been found, whilst within the Cave Oolite, the males are equally, if not more so, as common as the females.

## Genus *EKTYPHOCY THERE* nov.

DERIVATION OF NAME. Greek, *ἐκτυφῶν*, to puff up, + *cythere*.

DIAGNOSIS. Kirtonellinae, subtriangular to subrectangular, convex in dorsal view. Lateral border extended below ventral margin. Anterior and posterior marginal borders compressed. Slight swelling below anterior cardinal angle suggestive of eye swelling. Hinge antimerodont with broad, shelf-like accommodation groove in left valve. Left valve larger than right.

TYPE SPECIES. *Procytheridea triangula* Brand, 1961.

REMARKS. Externally *Ektyphocythere* resembles *Neocythere* Mertens, 1956, but differs principally in the possession of an antimerodont hinge. *Procytheridea* Peterson, 1954, is also similar, from which *Ektyphocythere* can be distinguished by the extension of the ventrolateral border below the ventral surface, possession of a U-shaped anterodorsal antennal muscle scar, and the development of a much more strongly convex carapace (in dorsal view).

Several species of *Procytheridea* recorded from the Lias (Europe) by Apostolescu (1959), Klingler & Neuweiler (1959), and Martin (1960), from the Bajocian (Europe) by Brand & Malz (1961) and from the Bathonian (Europe) by Oertli (1960) resemble *Ektyphocythere* more closely than they do *Procytheridea*. In all cases a distinctive ornament of ridges arranged in a triangular pattern is present. These species are listed below :—



*Procytheridea luxuriosa* Apostolescu  
*P. vitiosa* Apostolescu  
*P. betzi* Klingler & Neuweiler  
*P. triebeli* Klingler & Neuweiler  
*P. laqueata* Klingler & Neuweiler  
*P. spinaecostata* Klingler & Neuweiler  
 ? *P. arcuatocostata* Martin  
*P. parva* Oertli  
*Procytherida triangula* Brand

Variations in the ornament serve to distinguish the above species from *E. triangula*. The ostracod *Neocythere* ? *n.sp.* Oertli (1958, pl. 5, figs. 125-128) from the Aptian-Albian of southern France, closely resembles the large adults of *E. triangula* and is possibly congeneric. If a closer relationship between *Ektyphocythere* and *Neocythere* can be shown it may be preferable to consider the former as a subgenus of the latter.

Dr. G. A. Cooper of the Smithsonian Institution, Washington, U.S.A., kindly sent me specimens of *Procytheridea exempla* Peterson (locality Js-XV j, see Peterson, 1954: 156) and *P. crassa* Peterson (locality Js-XVIII c) to examine. In both cases the ostracods came from the same level as the holotype. This examination has shown that many of the European species placed in *Procytheridea* are not congeneric with the type species, *P. exempla*. Some almost certainly belong to *Ektyphocythere*. In addition, *P. crassa* is definitely not congeneric with *P. exempla* and should be removed from the genus. This is true also of the European species placed in *Procytheridea* on their resemblance to *P. crassa*.

### ***Ektyphocythere triangula* (Brand)**

(Pl. 15, figs. 5-18; Text-fig. 13)

1961. *Procytheridea triangula* Brand, p. 161, pl. 1, figs. 11-14.

EMENDED DIAGNOSIS. A species of *Ektyphocythere* with prominent triangular ornament of coarse ridges breaking down medially to produce reticulation. Ventro-lateral border extended below ventral surface, alaeform in large adults.

DESCRIPTION. Carapace subtriangular to subquadrate in outline with the ventro-lateral border extended below the ventral surface. Carapace strongly convex as seen in dorsal view. Greatest length extends through midpoint, greatest height slightly anterior of middle, greatest width in the posterior third in adult instars but tends to be more to the centre of the carapace in pre-adult instars. Shell surface ornamented by 3-4 coarse ridges situated obliquely in the anterodorsal and anteroventral parts of the carapace and continued ventrolaterally as longitudinal ridges. At the centre of this triangular arrangement the ridges tend to break up into a coarse reticulation. A slight swelling just below the anterior cardinal angle probably represents an eye swelling. The normal pore canals, when visible, rather large and circular, evenly spaced over the carapace. Ventrally each valve possesses



3 longitudinal ridges. Valve margins compressed with a thickened marginal rim. *Left valve* larger than the right which it overlaps midventrally and overreaches terminally. Dorsally the right valve overreaches the left. The dorsal margin in the left valve almost uniformly convex in pre-adult instars becoming rather more undulating with a median concavity in the larger adults. In the *right valve* a dorso-median bulge of the carapace projects above the dorsal margin, the latter tending to be straight or slightly convex. Anterior rounded, posterior triangular, the posterodorsal slope of the right valve being slightly more concave than in the left. Ventral margin convex with the valvular incurvature median or slightly in front of middle. *Hinge* antimerodont with terminal dentate ridges (with approximately 5 teeth) and a loculate median groove in the right valve. Left valve with the corresponding terminal loculate sockets and a dentate median bar above which is an elongate accommodation groove. *Inner margin* and *line of concrescence* coincide, the duplicature being quite broad. *Radial pore canals* straight and few in number, widely spaced and numbering 8–10 anteriorly and approximately 3 posteriorly. The selvage is prominent around the free margin, outside of which a flange is developed around the anterior and posterior margins. *Muscle scars* consist of a subvertical row of 4 oval adductor scars with a single U-shaped anterodorsal antennal scar and an oval anteroventral mandibular scar.

### Dimensions

Io. 622 carapace (Pl. 15, figs. 8, 9), length 0.65 mm.; height 0.37 mm.; width 0.39 mm.

Io. 623 right valve (Pl. 15, fig. 5), length 0.64 mm.; height 0.35 mm.

Io. 624 left valve, length 0.73 mm.; height 0.45 mm.

Io. 625 right valve (Pl. 15, figs. 11, 14), length 0.51 mm.; height 0.31 mm.

Io. 626 left valve (Pl. 15, figs. 10, 13), length 0.52 mm.; height 0.35 mm.

Io. 627 carapace (Pl. 15, figs. 7, 12, 15, 17), length 0.52 mm.; height 0.33 mm.; width 0.33 mm.

Io. 692 right valve (Pl. 15, fig. 18), length 0.44 mm.; height 0.25 mm.

Io. 695 left valve (Pl. 15, fig. 16; Text-fig. 13), length 0.50 mm.; height 0.30 mm.

REMARKS. The specimens described here from the Kirton Shale, Kirton Lindsey, are certainly conspecific with *Procytheridea triangula* Brand, being identical with the specimens described by Brand (1961: 162, pl. 1, figs. 11–14) at the size range indicated, namely, length 0.47–0.51 mm. However, Brand does not mention larger adult instars which here differ quite considerably morphologically and attain a length of 0.73 mm. The most striking difference in these larger specimens is the increase in the ventrolateral extension of the valve. In addition the anterior ornamentation may become greatly reduced and the muscle scars show up as raised spots on the valve surface. The adult specimens of *E. triangula* bear little resemblance to the genus *Procytheridea* and compared with the smaller instars are relatively uncommon. Because of this latter factor it may be possible that those species mentioned previously which bear a resemblance to *E. triangula* might well possess larger instars as yet undescribed.



Family **LOXOCONCHIDAE** Sars, 1925Genus **CYTHEROMORPHA** Hirschmann, 1909***Cytheromorpha* (?) *greetwellensis* sp. nov.**

(Pl. 15, figs. 19-21)

DIAGNOSIS. *Cytheromorpha*?, small, elongate, carapace constricted medially by broad midventral depression. Surface finely pitted, producing an almost reticulate appearance.

HOLOTYPE. Io. 620, Kirton Cementstone Series, Greetwell Quarry, Lincoln.

PARATYPE. Io. 621, Kirton Shale, Kirton Cement Quarry, Kirton Lindsey.

DESCRIPTION. *Carapace* subrectangular in outline, tapering to the posterior. Greatest length extending through midpoint, greatest height at the anterior cardinal angle, greatest width situated in the posterior third. In dorsal view the ostracod is slender and almost parallel-sided with a slight median constriction. Dorsal margin straight, sloping slightly to the posterior. Cardinal angles distinct, rather broad. Ventral margin flattened medially, tending to be slightly concave, but convex anteroventrally and posteroventrally. Anterior high and uniformly rounded, posterior triangular with a short and straight, steeply angled posterodorsal slope and a short, slightly convex posteroventral slope. A slight swelling extends along the ventrolateral part of the carapace. Shell surface uniformly ornamented with small, closely set, circular pits, producing an almost reticulate appearance. Valves almost equi-valve although the left valve slightly overlaps the right midventrally. Dorsally the right valve slightly overreaches the left. Internal characters not seen.

*Dimensions*

HOLOTYPE. Io. 620, carapace (Pl. 15, figs. 19-21), length 0.43 mm.; height 0.20 mm.; width 0.17 mm.

PARATYPE. Io. 621, carapace, length 0.40 mm.; height 0.18 mm.; width 0.13 mm.

REMARKS. A rare ostracod which in general shape closely resembles *Cytherura* (?) *liesbergensis* Oertli (1959a, pl. 4, figs. 112-125) but lacks the sharply differentiated marginal area and median sulcus present in the latter species. The caudal process, common to the genus *Cytherura*, is not represented here, the species being assigned to the genus *Cytheromorpha* which it externally resembles.

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## EXPLANATION OF PLATES

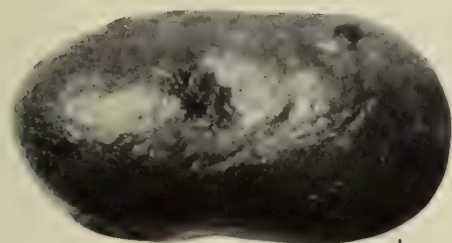
All specimens illustrated are now in the Department of Palaeontology, British Museum (Natural History). The photographs, taken by the author, are unretouched except where stated. Dark stained ostracods have been treated with silver nitrate solution to bring out surface detail. Photographs of muscle scars and pore canals taken with the specimen immersed in glycerine.



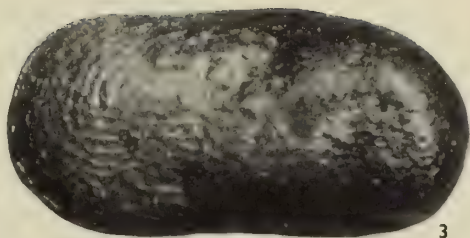
# PLATE 1

|             |                                                                                                                   |      |
|-------------|-------------------------------------------------------------------------------------------------------------------|------|
|             |                                                                                                                   | page |
|             | <i>Cytherella fullonica</i> Jones & Sherborn . . . . .                                                            | 184  |
| FIGS. 1, 2. | External and internal views of right valve, Kirton Shale, Kirton Lindsey. Io. 520. $\times 85$ .                  |      |
|             | <i>Cytherelloidea catenulata</i> (Jones & Sherborn) . . . . .                                                     | 184  |
|             | Specimens from the Kirton Shale, Kirton Lindsey.                                                                  |      |
| FIGS. 3, 5. | External and internal views of left valve. Io. 524. $\times 85$ .                                                 |      |
| FIGS. 4, 6. | External and internal views of right valve. Io. 525. $\times 85$ .                                                |      |
|             | <i>Platella jurassica</i> sp. nov. . . . .                                                                        | 185  |
| FIGS. 7-10. | Left, right, dorsal and ventral views of carapace. Kirton Shale, Kirton Lindsey. Holotype, Io. 526. $\times 85$ . |      |

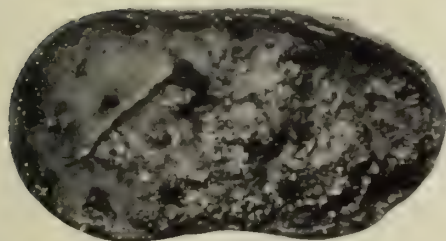




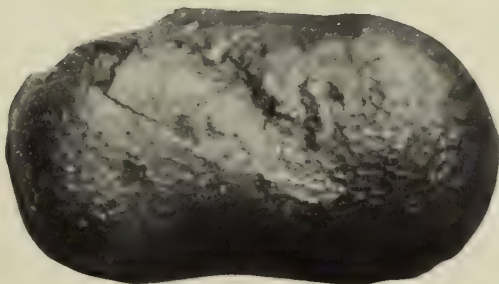
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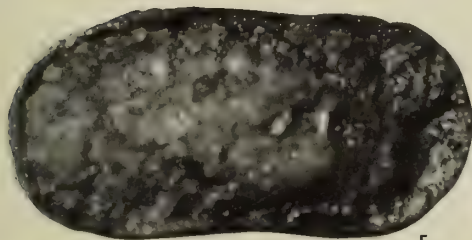
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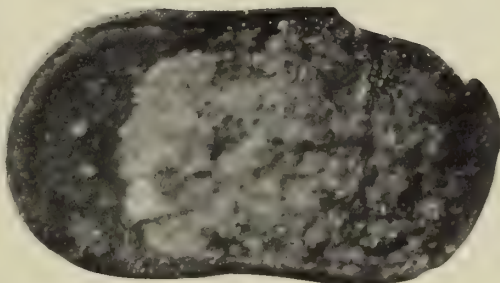
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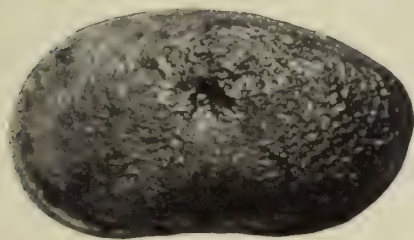
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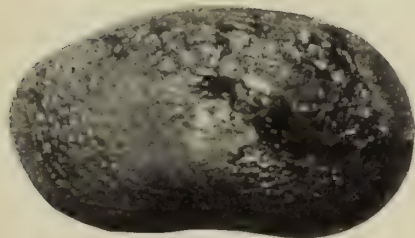
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# PLATE 2

*Paracypris bajociana* sp. nov. . . . . page  
186

FIGS. 1, 3-6, 8, from the Kirton Shale, Kirton Lindsey.

FIGS. 2, 7, from the marl bed below the Cave Oolite, South Cave.

FIGS. 1, 3, 4. Right, dorsal and ventral views of carapace. Holotype, Io. 528.  $\times 85$ .

FIG. 2. Left valve showing branching radial pore canals. Paratype, Io. 529.  $\times 85$ .

FIGS. 5, 6. Left valve showing muscle scars. Paratype, Io. 532. FIG. 5.  $\times 85$ . FIG. 6, muscle scars enlarged.  $\times 200$ .

FIG. 7. Internal view, left valve, showing terminal vestibules and radial pore canals. Paratype, Io. 530.  $\times 85$ .

FIG. 8. Internal view of left valve showing simple hinge groove. Paratype, Io. 533.  $\times 85$ .

*Bairdia hilda* Jones . . . . . 188

Specimens from the Kirton Shale, Kirton Lindsey.

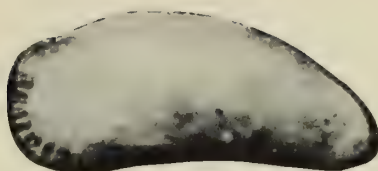
FIGS. 9, 11, 12. Left, dorsal and ventral views of complete carapace. I. 535.  $\times 65$ .

FIG. 10. External view, right valve. Io. 537.  $\times 65$ .





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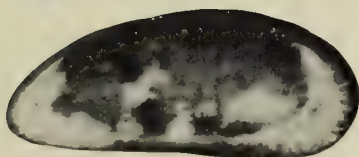
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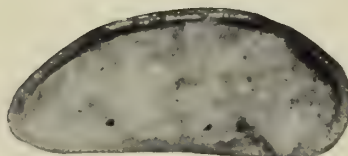
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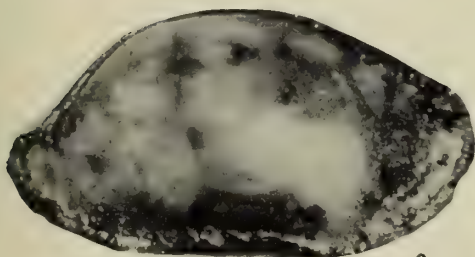
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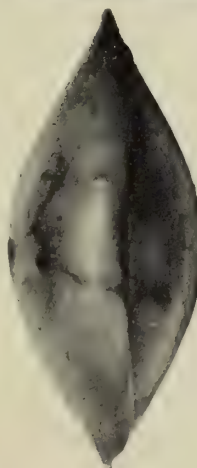
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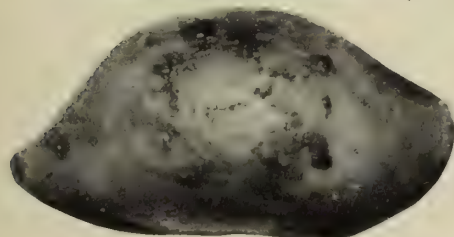
9



11



12



10











# PLATE 3

*Bairdia hilda* Jones . . . . . page  
188

Specimens from the Kirton Shale, Kirton Lindsey.

FIG. 1. Internal view, right valve. Io. 537.  $\times 65$ .

FIGS. 2, 3. External and internal views, left valve. Io. 536.  $\times 65$ .

FIG. 4. Muscle scars on internal cast. Io. 534.  $\times 180$ .

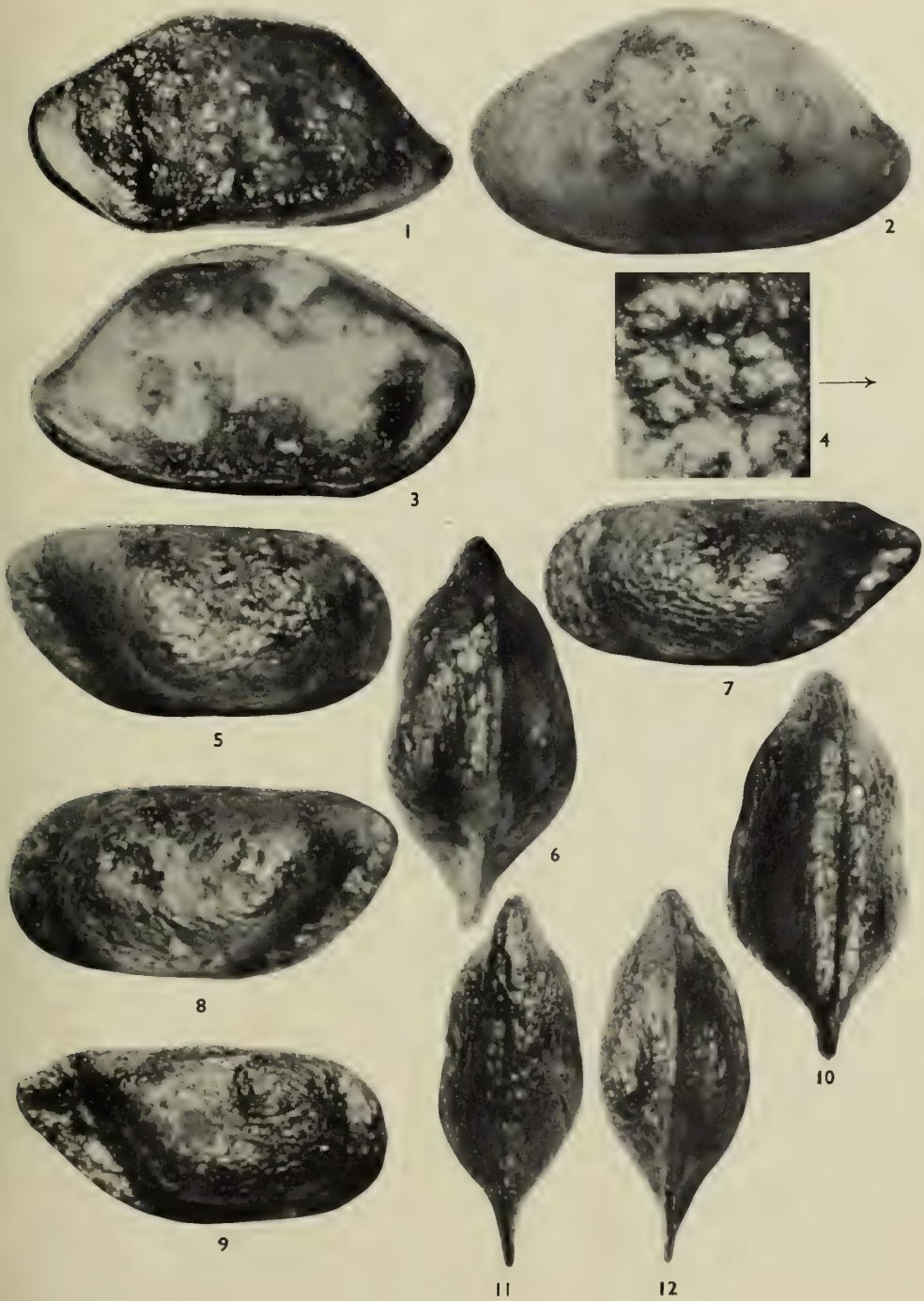
*Monoceratina vulsa* (Jones & Sherborn) . . . . . 189

Specimens from the Kirton Shale, Kirton Lindsey.

FIGS. 5, 6, 8, 10. Right, ventral, left and dorsal views of female ? carapace. Io. 539.  $\times 85$ .

FIGS. 7, 9, 11, 12. Left, right, dorsal and ventral views of male ? carapace. Io. 540.  $\times 85$ .















# PLATE 4

|                                                                                |      |
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|                                                                                | page |
| <i>Monoceratina</i> sp. cf. <i>M. scrobiculata</i> Triebel & Bartenstein . . . | 190  |

FIGS. 1-4. Left, right, dorsal and ventral views of juvenile carapace. Kirton Shale, Kirton  
Kirton Lindsey. Io. 538.  $\times 150$ .

|                                                 |     |
|-------------------------------------------------|-----|
| <i>Progonocythere cristata</i> sp. nov. . . . . | 191 |
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Specimens from the Kirton Shale, Kirton Lindsey.

FIGS. 5-8. Right, left, dorsal and ventral views of female carapace. Holotype, Io. 543.  
 $\times 85$ .

FIGS. 9, 10. Right and left views of male carapace. Paratype, Io. 544.  $\times 85$ .

FIG. 11. Hinge of female left valve. Paratype, Io. 546,  $\times 100$ .

FIGS. 12, 13. Left and right views of "juvenile" female carapace. Paratype, Io. 547.  
 $\times 85$ .

FIGS. 14, 15. Right and left views of "juvenile" male carapace. Paratype, Io. 548.  $\times 85$ .



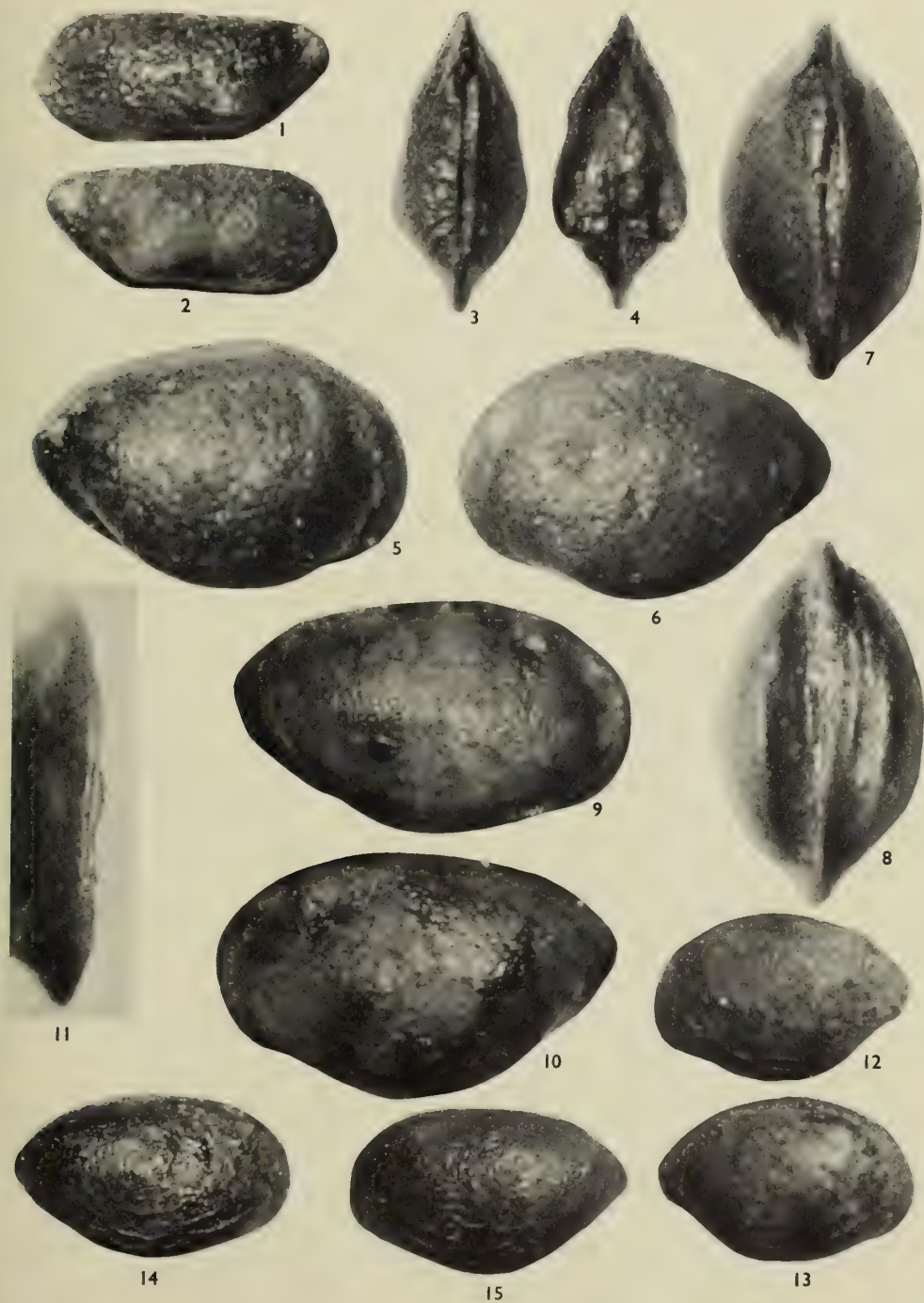












PLATE 5

*Progonocythere cristata* sp. nov. . . . . page  
191

Specimens from the Kirton Shale, Kirton Lindsey.

FIG. 1. Right valve, male, showing large normal pore canals. Paratype, Io. 549.  $\times 85$ .

FIG. 2. Left side of female carapace showing muscle scars. Paratype, Io. 550.  $\times 85$ .

FIGS. 3, 4. Dorsal and ventral views of "juvenile" male carapace. Paratype, Io. 548.  
 $\times 85$ .

FIG. 5. Internal view, right valve male. Paratype, Io. 545.  $\times 85$ .

FIG. 6. Internal view, left valve female. Paratype, Io. 546.  $\times 85$ .

*Pneumatocythere bajociana* gen. et sp. nov. . . . . 193

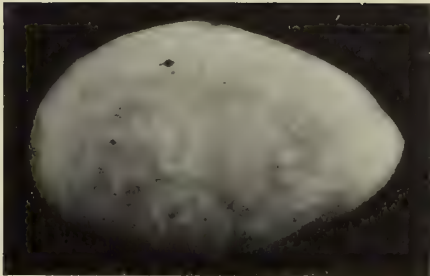
Specimens from the Yons Nab Beds, Yons Nab headland.

FIGS. 7-10. Right, left, dorsal and ventral views of female carapace. Holotype, Io. 551.  
 $\times 70$ .





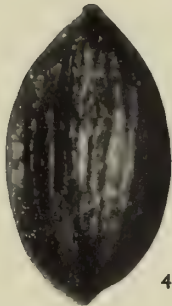
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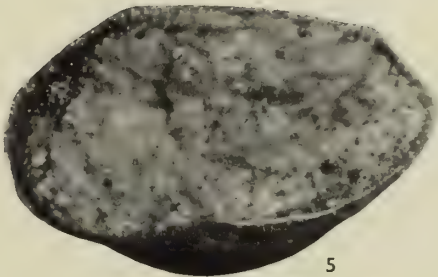
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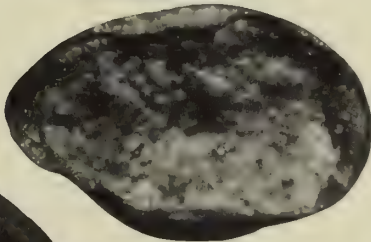
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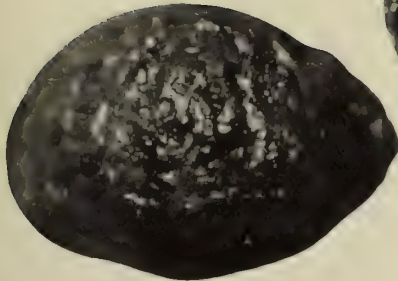
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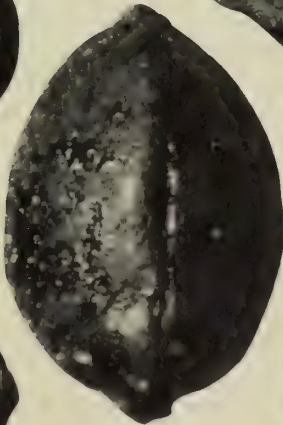
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6



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9



10











PLATE 6

*Pneumatocythere bajociana* gen. et sp. nov. . . . . page  
193

FIGS. 1-7, 9 from the Yons Nab Beds, Yons Nab headland.

FIGS. 8, 10, from the marl bed below the Cave Oolite, South Cave.

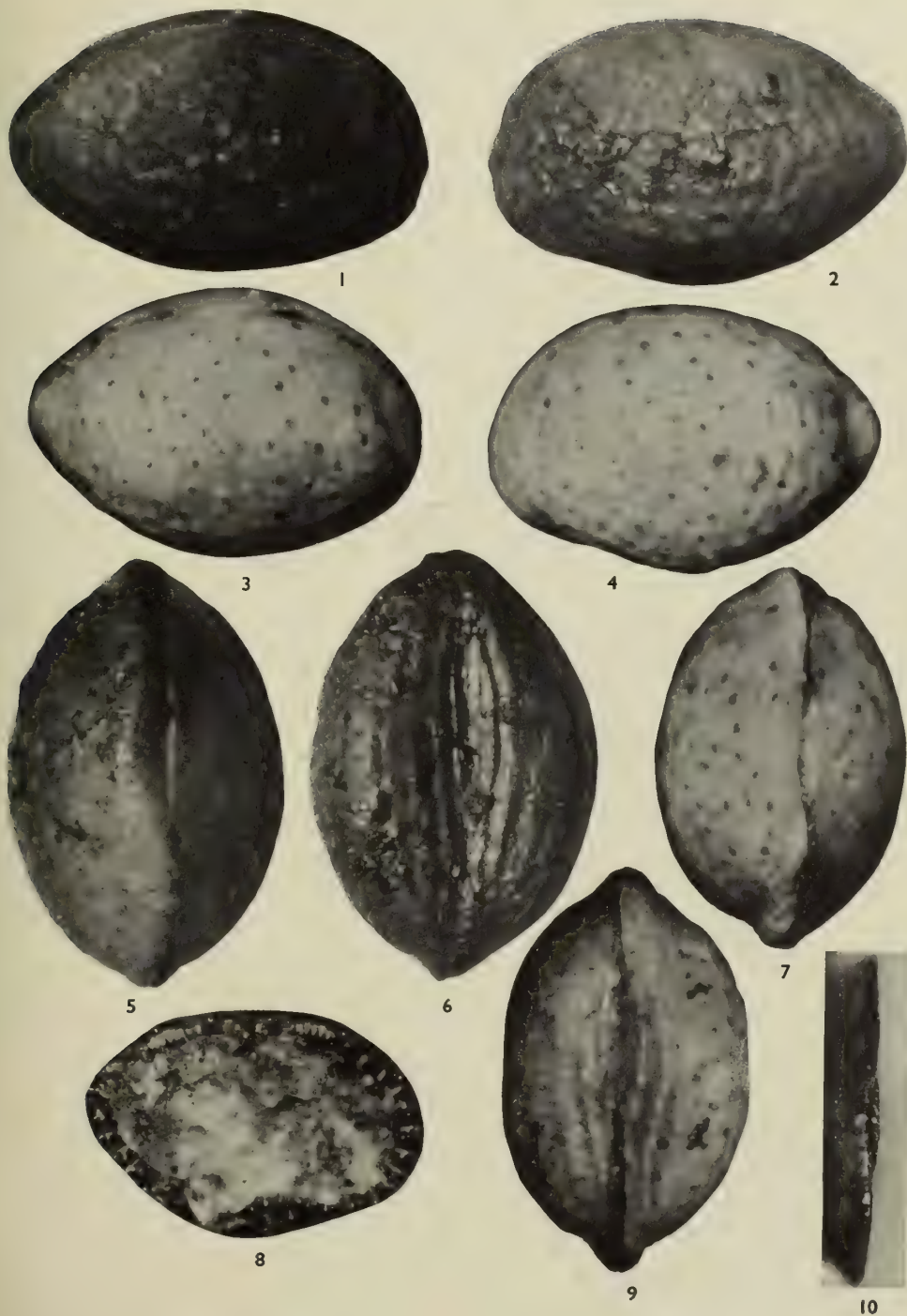
FIGS. 1, 2, 5, 6. Right, left, dorsal and ventral views of male carapace. Paratype, Io. 552.  
×70.

FIGS. 3, 4, 7, 9. Right, left, dorsal and ventral views of female carapace. Paratype, Io. 553.  
×70.

FIG. 8. Internal view, left valve, female, showing radial pore canals. Paratype, Io. 556.  
×70.

FIG. 10. Dorsal view of hinge, left valve, female. Paratype, Io. 556. ×70.















# PLATE 7

*Pneumatocythere bajociana* gen. et sp. nov. . . . . page  
193

FIGS. 1-3, from the marl bed below the Cave Oolite.

FIG. 4, from the Kirton Cementstone Series, Lincoln.

FIG. 1. Muscle scars on the exterior of a juvenile carapace. Paratype, Io. 555.  $\times 170$ .

FIG. 2. Muscle scars on the exterior of a female left valve. Paratype, Io. 554.  $\times 170$ .

FIG. 3. Internal view, left valve, female. Paratype, Io. 556.  $\times 70$ .

FIG. 4. Internal view, juvenile right valve. Paratype, Io. 557.  $\times 70$ .

*Acanthocythere* (*Protoacanthocythere*) *faveolata* subgen. et sp. nov. . . . . 195

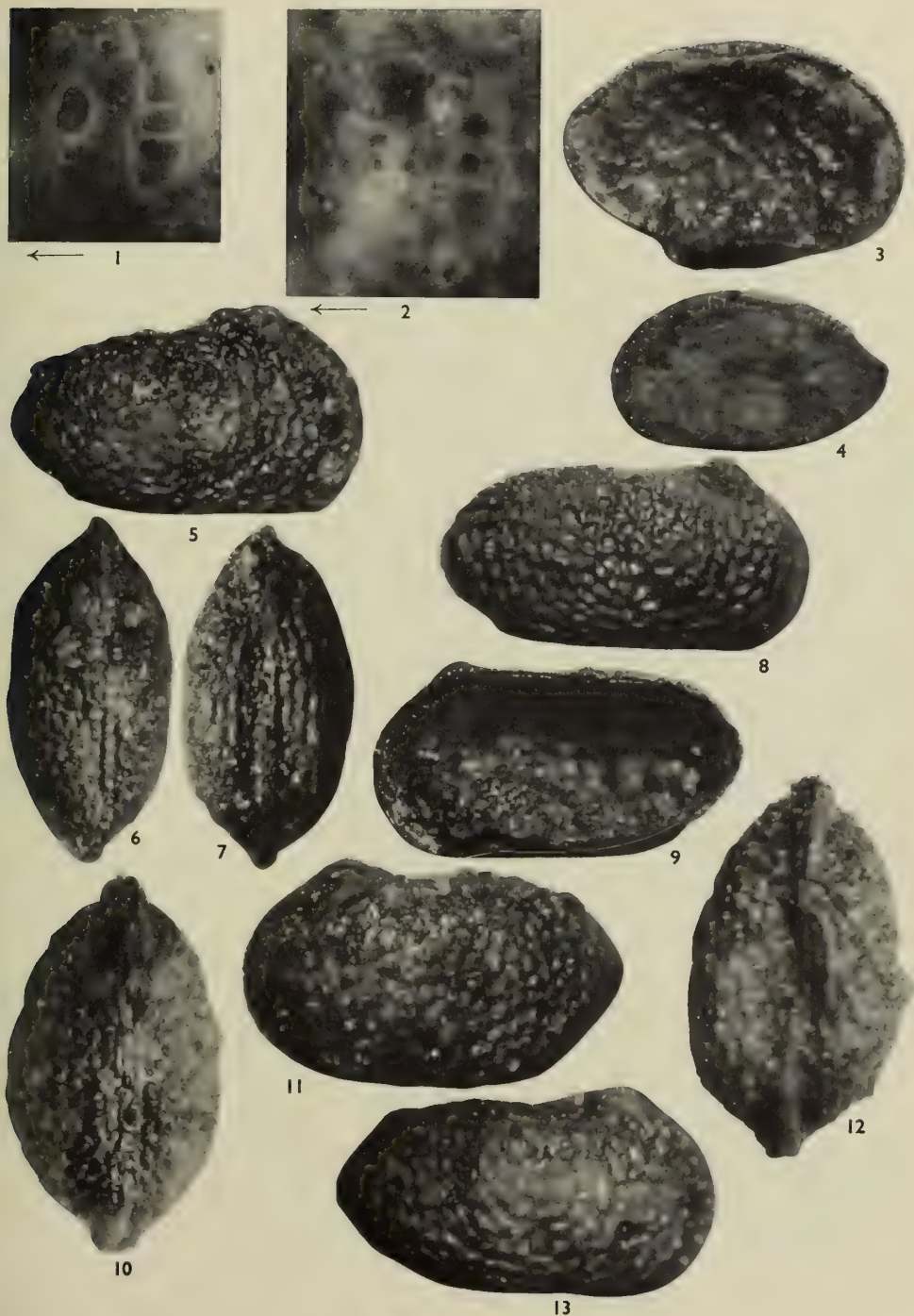
Specimens from the Kirton Shale, Kirton Lindsey.

FIGS. 5-7. Right, dorsal and ventral views of female carapace. Holotype, Io. 558.  $\times 85$ .

FIGS. 8, 9. External and internal views of male right valve. Paratype, Io. 561.  $\times 85$ .

FIGS. 10-13. Dorsal, left, ventral and right views of male carapace. Paratype, Io. 559.  $\times 85$ .















# PLATE 8

|                                                                                                   | page |
|---------------------------------------------------------------------------------------------------|------|
| <i>Acanthocythere</i> ( <i>Protoacanthocythere</i> ) <i>faveolata</i> subgen. et sp. nov. . . . . | 195  |

Specimens from the Kirton Shale, Kirton Lindsey.

- FIG. 1. Internal view of female right valve. Paratype, Io. 563.  $\times 85$ .  
 FIG. 2. Internal view of male left valve. Paratype, Io. 560.  $\times 85$ .  
 FIGS. 3, 4. Muscle scars (retouched) on the exterior of a male right valve. Paratype, Io. 564.  
 Fig. 3.  $\times 130$ ; Fig. 4.  $\times 85$ .  
 FIG. 5. Internal view, left valve male, showing radial pore canals. Paratype, Io. 565.  $\times 85$ .

|                                                                                 |     |
|---------------------------------------------------------------------------------|-----|
| <i>Fuhrbergiella</i> ( <i>Praefuhrbergiella</i> ) <i>arens</i> sp. nov. . . . . | 197 |
|---------------------------------------------------------------------------------|-----|

FIGS. 6, 7, 9, from the Kirton Cementstone Series, Kirton Lindsey.

FIGS. 8, 10-15, from the Kirton Shale, Kirton Lindsey.

- FIG. 6. Left valve (hinge), female. Paratype, Io. 569.  $\times 85$ .  
 FIG. 7. Right valve (hinge), female. Paratype, Io. 568.  $\times 85$ .  
 FIG. 8. Right valve (hinge), male. Paratype, Io. 567.  $\times 85$ .  
 FIG. 9. Internal view, left valve, female, showing radial pore canals. Paratype, Io. 570.  
 $\times 85$ .  
 FIGS. 10, 13. External and internal views of male right valve. Paratype, Io. 567.  $\times 85$ .  
 FIGS. 11, 12, 14, 15. Right, ventral, left and dorsal views of female carapace. Holotype,  
 Io. 566.  $\times 85$ .



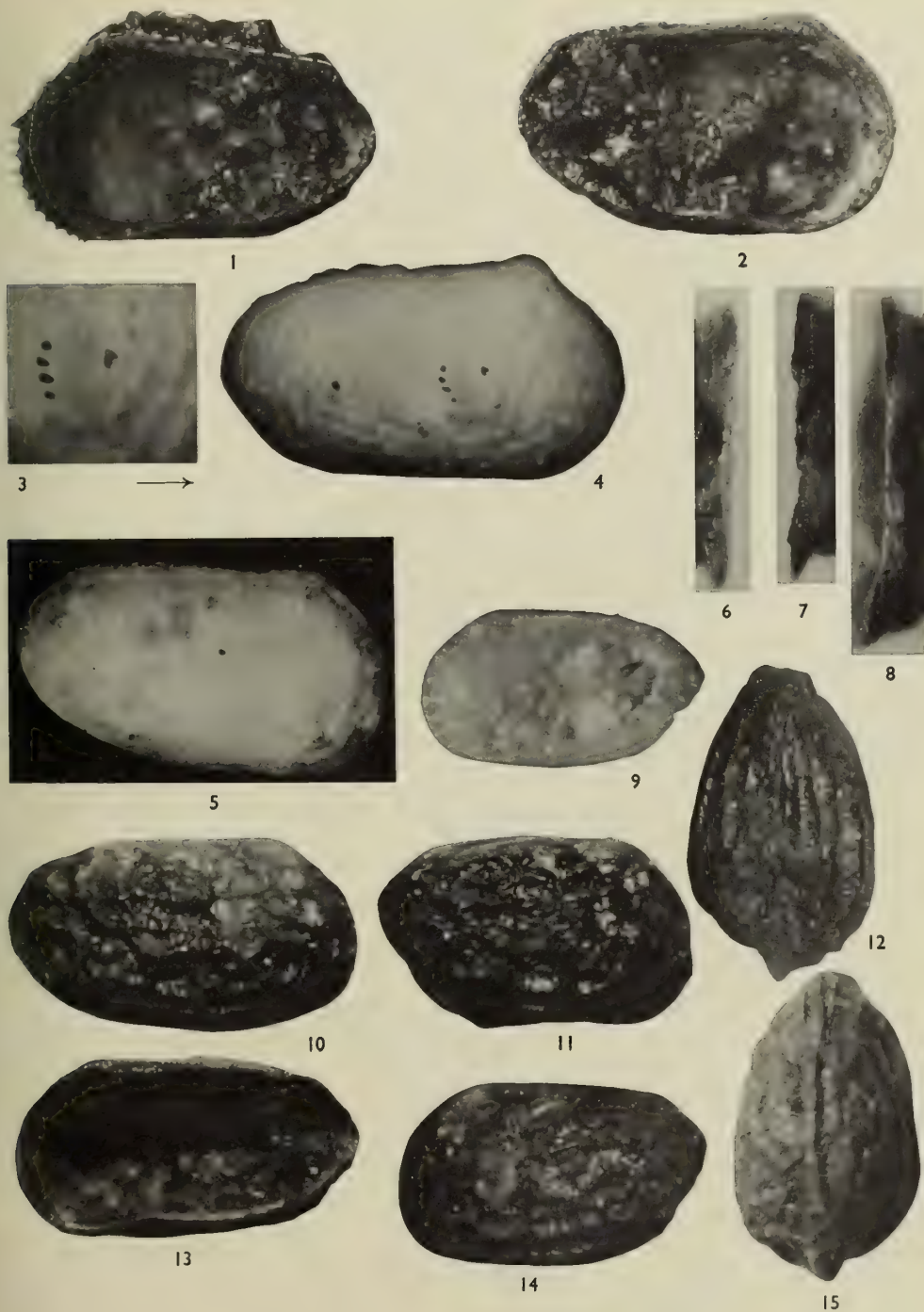












PLATE 9

|                                                         |             |
|---------------------------------------------------------|-------------|
| <i>Fuhrbergiella (Praefuhrbergiella) arens</i> sp. nov. | page<br>197 |
|---------------------------------------------------------|-------------|

Specimens from the Kirton Cementstone Series, Kirton Lindsey.

- FIG. 1. Internal view, right valve female. Paratype, Io. 568.  $\times 85$ .  
 FIG. 2. Internal view, left valve, female. Paratype, Io. 569.  $\times 85$ .  
 FIG. 3. Muscle scars, right valve, female. Paratype, Io. 568.  $\times 100$ .

|                                                |     |
|------------------------------------------------|-----|
| <i>Aulacocythere punctata</i> gen. et sp. nov. | 199 |
|------------------------------------------------|-----|

Specimens from the Kirton Shale, Kirton Lindsey.

- FIG. 4. Muscle scars, right valve, male. Paratype, Io. 572.  $\times 180$ .  
 FIG. 5. Right valve, female. Paratype, Io. 573.  $\times 85$ .  
 FIGS. 6, 12. External and internal views, female left valve. Paratype, Io. 574.  $\times 85$ .  
 FIG. 7. Right valve (hinge), male. Paratype, Io. 572.  $\times 105$ .  
 FIGS. 8, 11, 14, 15. Left, right, dorsal and ventral views, male carapace. Holotype, Io. 571.  $\times 85$ .  
 FIG. 9. Left valve, male. Paratype, Io. 823.  $\times 85$ .

|                                                  |     |
|--------------------------------------------------|-----|
| <i>Aulacocythere reticulata</i> gen. et sp. nov. | 200 |
|--------------------------------------------------|-----|

Specimens from the Kirton Shale, Kirton Lindsey.

- FIGS. 10, 13, 20, 21. Left, right, dorsal and ventral views of female carapace. Holotype, Io. 575.  $\times 85$ .  
 FIGS. 16-19. Right, left, dorsal and ventral views of male carapace. Paratype, Io. 576.  $\times 85$ .  
 FIGS. 22. Internal view, right valve, male. Paratype, Io. 579.  $\times 85$ .  
 FIGS. 23, 24. Right and left views of juvenile carapace. Paratype, Io. 578.  $\times 85$ .  
 FIG. 25. Right valve (hinge), male. Paratype, Io. 579.  $\times 85$ .



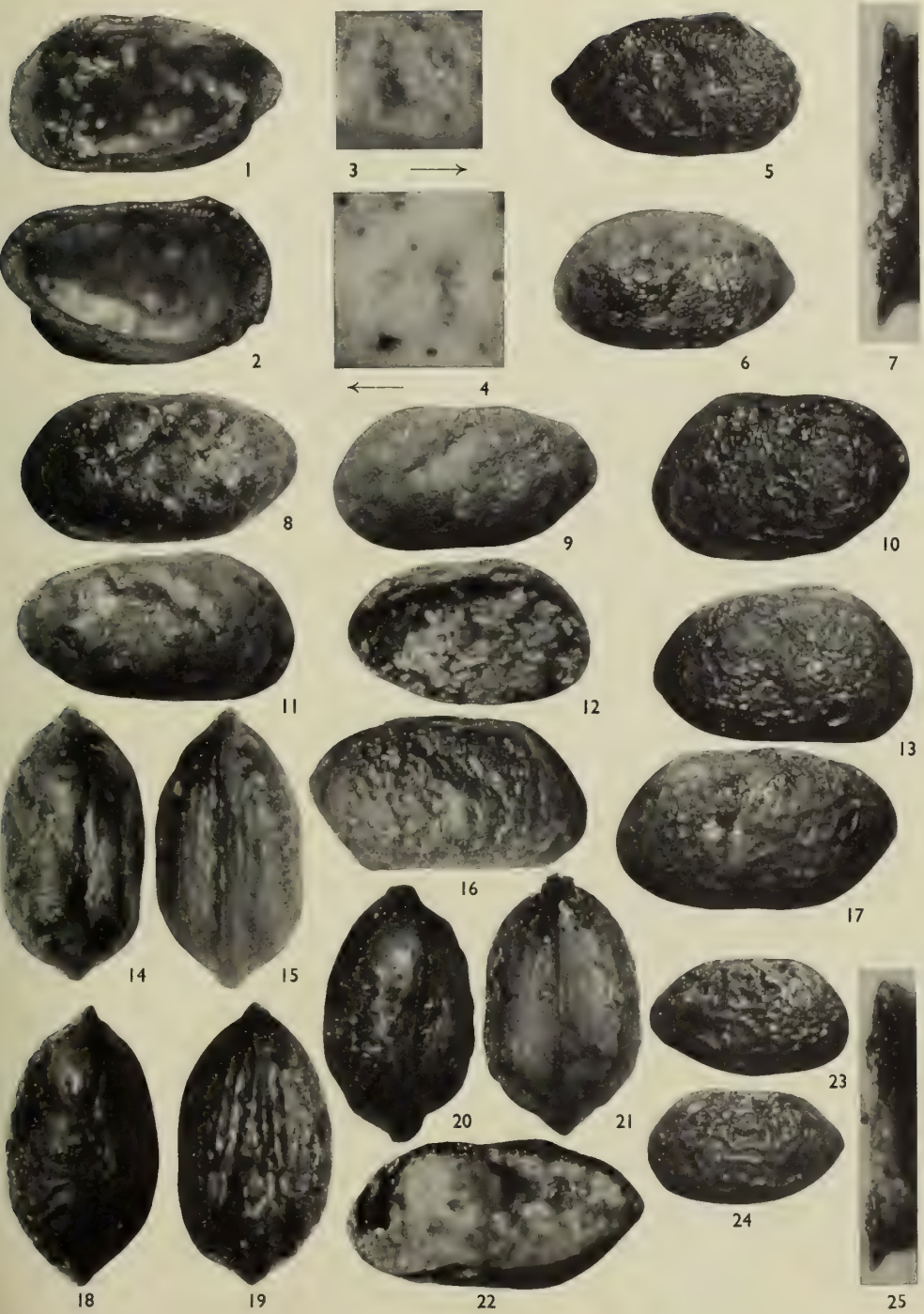












PLATE 10

|                                                          |      |
|----------------------------------------------------------|------|
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| <i>Aulacocythere reticulata</i> gen. et sp. nov. . . . . | 200  |

FIG. 1. Internal view of male left valve from the Kirton Shale, Kirton Lindsey. Paratype, Io. 577,  $\times 85$ .

|                                                    |     |
|----------------------------------------------------|-----|
| <i>Camptocythere lincolnensis</i> sp. nov. . . . . | 201 |
|----------------------------------------------------|-----|

Specimens from the Kirton Cementstone Series, Lincoln.

FIGS. 2-5. Left, dorsal, ventral and right views of carapace. Holotype, Io. 580.  $\times 85$ .

FIG. 6. Muscle scars (retouched), right valve. Paratype, Io. 583.  $\times 180$ .

FIGS. 7, 10. External and internal views of right valve. Paratype, Io. 583.  $\times 85$ .

FIGS. 8, 9. Internal and external views of left valve. Paratype, Io. 581.  $\times 85$ .

FIGS. 11, 12. Internal and external views of right valve (broken). Paratype, Io. 582.  $\times 85$ .

FIG. 13. Internal view of right valve showing radial pore canals. Paratype, Io. 583.  $\times 85$ .

|                                                   |     |
|---------------------------------------------------|-----|
| <i>Pleurocythere kirtonensis</i> sp. nov. . . . . | 203 |
|---------------------------------------------------|-----|

Specimens from the Kirton Shale, Kirton Lindsey.

FIGS. 14, 16. Left and right views of female carapace. Holotype, Io. 584.  $\times 85$ .

FIGS. 15, 17. Internal view of valve and dorsal view of hinge, left valve, female. Paratype, Io. 585.  $\times 85$ .

FIG. 18. Right valve (hinge), male. Paratype, Io. 586.  $\times 85$ .



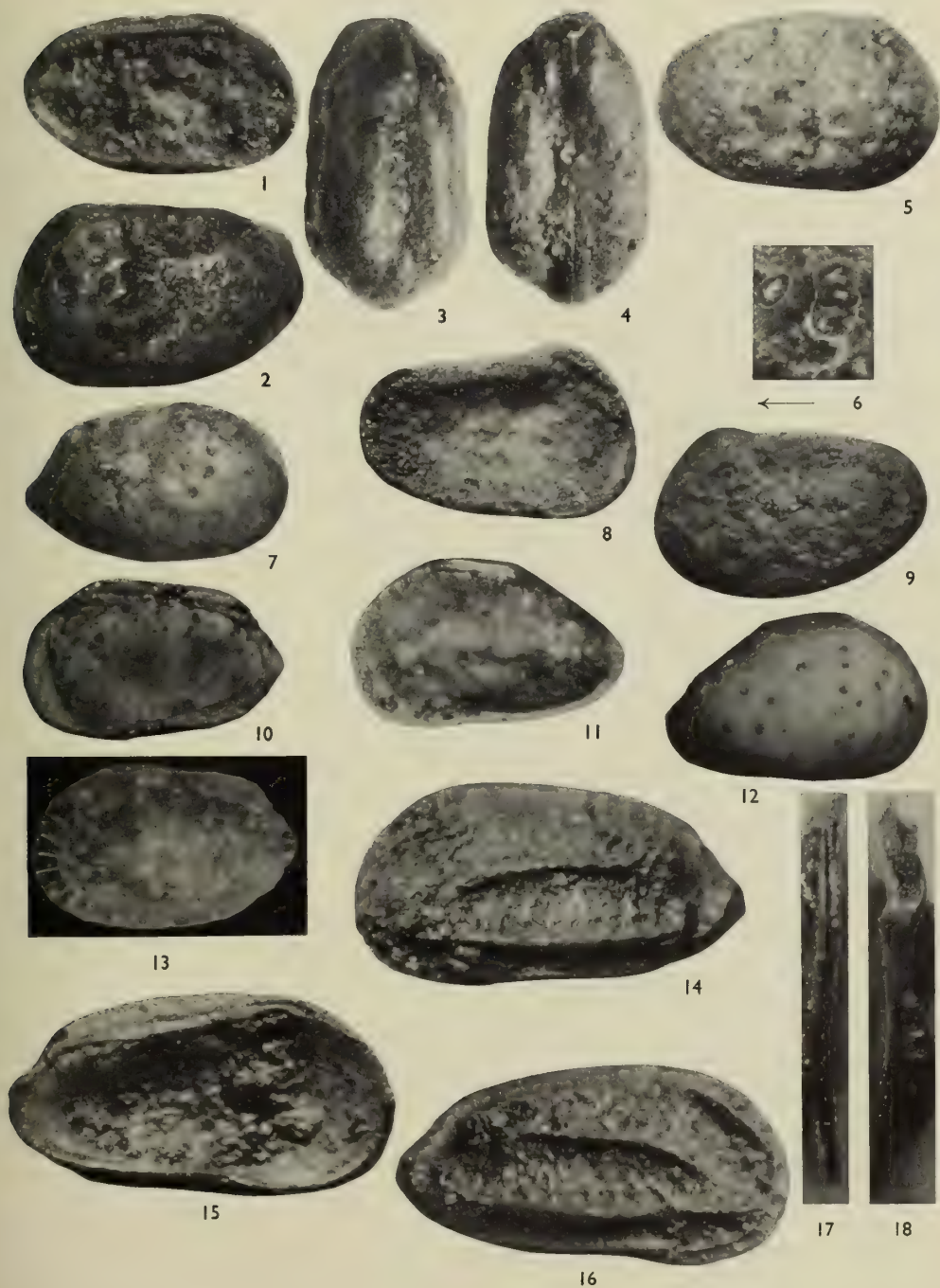












PLATE 11

|                                                   |      |
|---------------------------------------------------|------|
|                                                   | page |
| <i>Pleurocythere kirtonensis</i> sp. nov. . . . . | 203  |

Specimens from the Kirton Shale, Kirton Lindsey.

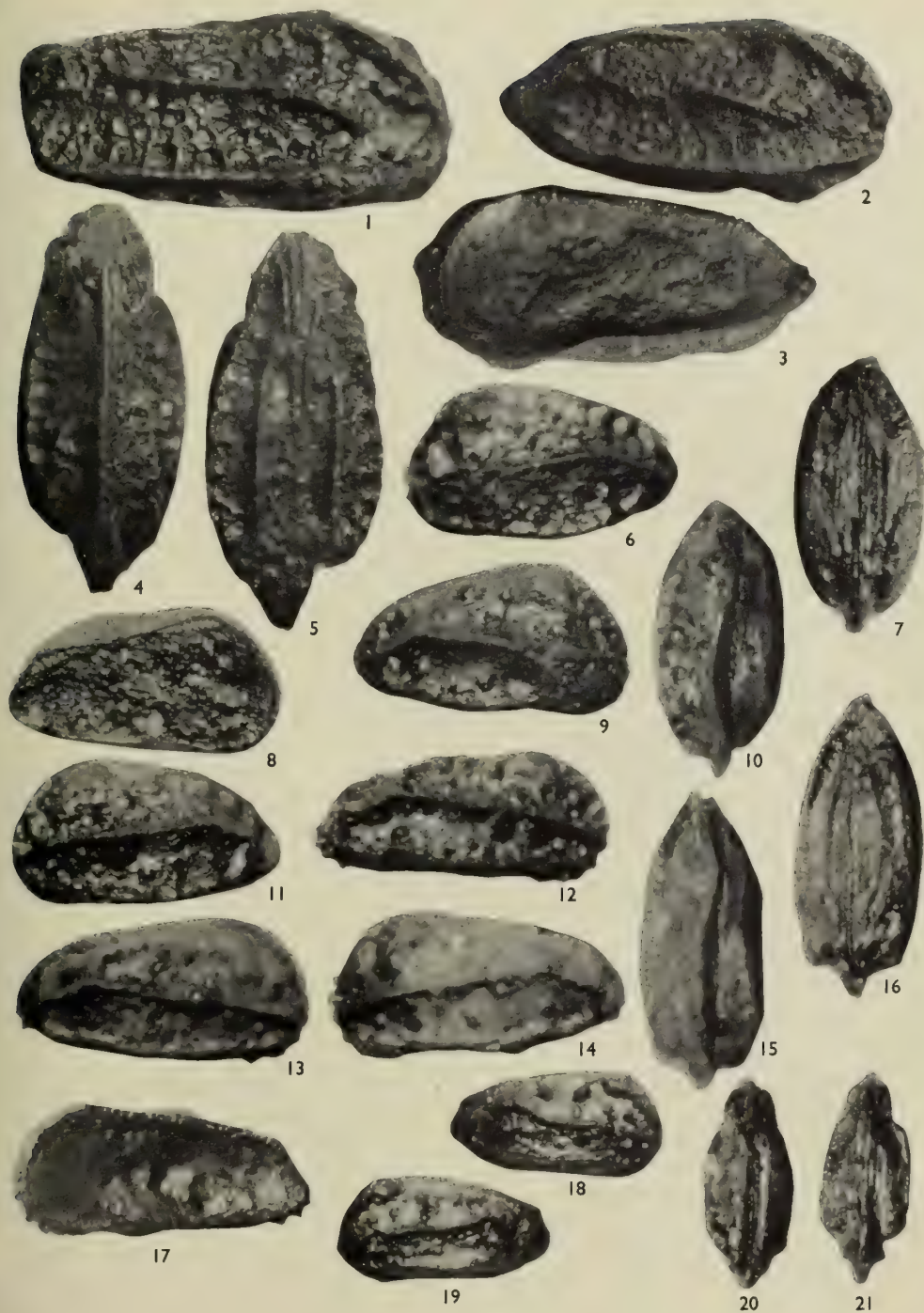
- FIG. 1. Right valve (broken), male. Paratype, Io. 587.  $\times 85$ .  
 FIGS. 2, 3. External and internal views, right valve, male. Paratype, Io. 586.  $\times 85$ .  
 FIGS. 4, 5. Dorsal and ventral views of female carapace. Holotype, Io. 584.  $\times 85$ .

|                                              |     |
|----------------------------------------------|-----|
| <i>Pleurocythere nodosa</i> sp. nov. . . . . | 204 |
|----------------------------------------------|-----|

Specimens from the Kirton Shale, Kirton Lindsey.

- FIGS. 6, 7, 9, 10. Left, ventral, right and dorsal views of female carapace. Holotype, Io 588.  $\times 85$ .  
 FIGS. 8, 11. Internal and external views of female left valve. Paratype, Io. 591.  $\times 85$ .  
 FIGS. 12, 17. External and internal views of male right valve. Paratype, Io. 590.  $\times 85$ .  
 FIGS. 13-16. Right, left, dorsal and ventral views of male carapace. Paratype, Io. 589.  $\times 85$ .  
 FIGS. 18-21. Right, left, dorsal and ventral views of juvenile carapace. Paratype, Io. 592.  $\times 85$ .















# PLATE 12

|                                              | page |
|----------------------------------------------|------|
| <i>Dolocythere maculosa</i> sp. nov. . . . . | 205  |

Specimens from the marl bed below the Cave Oolite, South Cave.

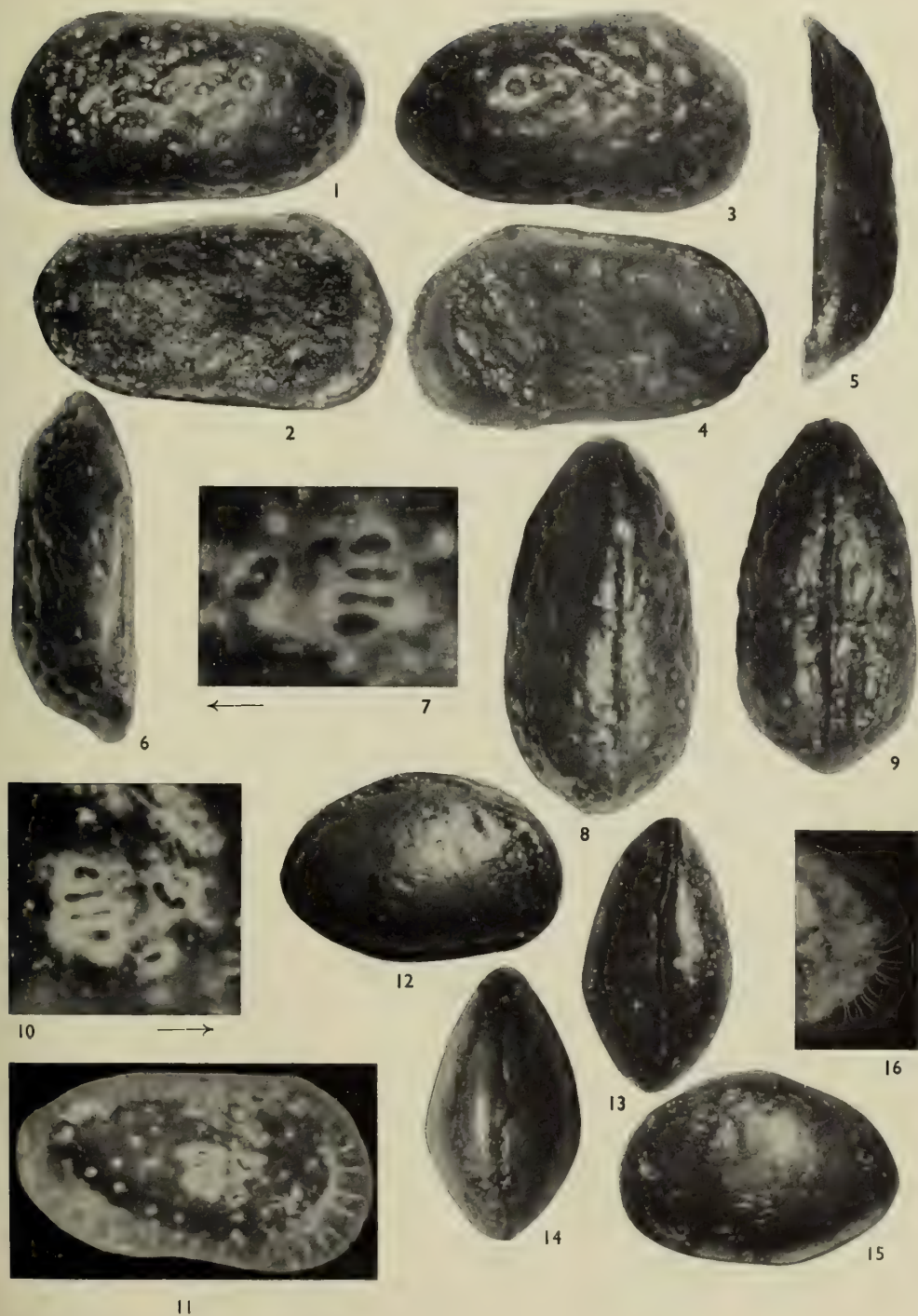
- FIGS. 1, 2, 6. External, internal and dorsal views of single left valve. Holotype, Io. 609.  $\times 85$ .  
 FIGS. 3-5. External, internal and dorsal views of single right valve. Paratype, Io. 611.  $\times 85$ .  
 FIG. 7. Muscle scars, right valve. Paratype, Io. 613.  $\times 260$ .  
 FIGS. 8, 9. Dorsal and ventral views of complete carapace. Paratype, Io. 610.  $\times 85$ .  
 FIG. 10. Muscle scars, left valve. Paratype, Io. 612.  $\times 220$ .  
 FIG. 11. Muscle scars and radial pore canals, left valve. Paratype, Io. 612.  $\times 85$ .

|                                                                        |     |
|------------------------------------------------------------------------|-----|
| <i>Praeschuleridea subtrigona</i> (Jones & Sherborn) gen. nov. . . . . | 207 |
|------------------------------------------------------------------------|-----|

Specimens from the Kirton Shale, Kirton Lindsey.

- FIGS. 12-15. Right, ventral, dorsal and left views of female carapace. Io. 597.  $\times 85$ .  
 FIG. 16. Radial pore canals (anterior), left valve female (slightly retouched). Io. 595.  $\times 100$ .















# PLATE 13

|                                                                        |             |
|------------------------------------------------------------------------|-------------|
| <i>Praeschuleridea subtrigona</i> (Jones & Sherborn) gen. nov. . . . . | page<br>207 |
|------------------------------------------------------------------------|-------------|

Specimens from the Kirton Shale, Kirton Lindsey.

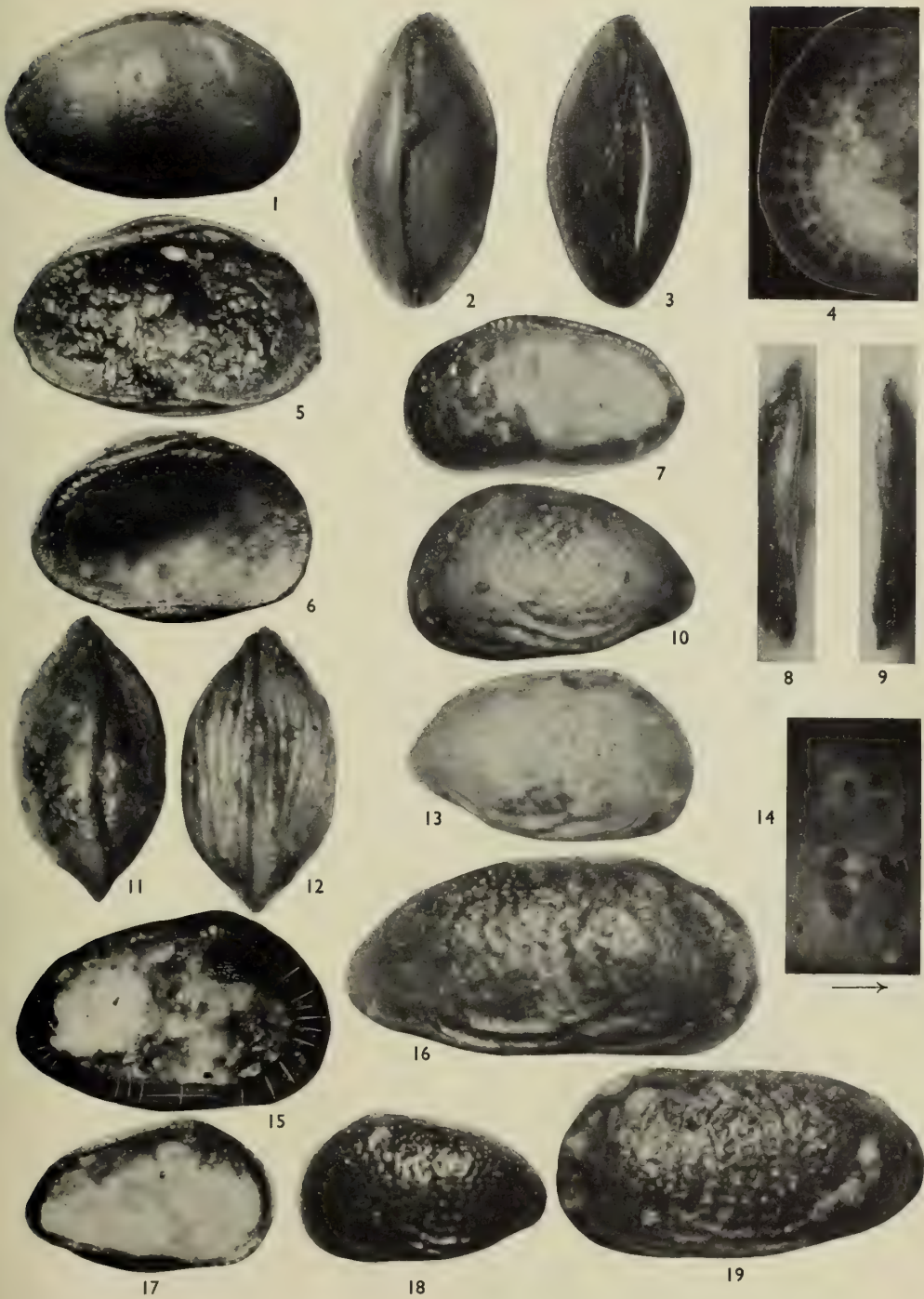
- FIGS. 1-3. Right, dorsal and ventral views of male carapace. Io. 596.  $\times 85$ .
- FIG. 4. Anterior radial pore canals, right valve, female. Io. 594.  $\times 100$ .
- FIGS. 5, 8. Internal and dorsal views of left valve, female. Io. 599.  $\times 85$ .
- FIG. 6. Internal view, left valve, female. Io. 593.  $\times 85$ .
- FIGS. 7, 9. Internal and dorsal views of right valve, male. Io. 598.  $\times 85$ .

|                                                    |     |
|----------------------------------------------------|-----|
| <i>Kirtonella plicata</i> gen. et sp. nov. . . . . | 210 |
|----------------------------------------------------|-----|

Specimens from the Kirton Shale, Kirton Lindsey.

- FIGS. 10-13. Left, dorsal, ventral and right views of female carapace. Holotype, Io. 600.  $\times 85$ .
- FIG. 14. Muscle scars, left valve, female. Paratype, Io. 608.  $\times 120$ .
- FIGS. 15. Internal view, left valve, female, showing radial pore canals (slightly retouched). Paratype, Io. 607.  $\times 85$ .
- FIG. 16. External view, right valve, male. Paratype, Io. 603.  $\times 85$ .
- FIGS. 17, 18. Internal and external views, left valve, female. Paratype, Io. 605.  $\times 85$ .
- FIG. 19. External view, left valve, male. Paratype, Io. 602.  $\times 85$ .















# PLATE 14

|                                                    | page |
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| <i>Kirtonella plicata</i> gen. et sp. nov. . . . . | 210  |

Specimens from the Kirton Shale, Kirton Lindsey.

- FIGS. 1, 2. Dorsal and ventral views of male carapace. Paratype, Io. 604.  $\times 85$ .
- FIGS. 3, 11. Internal and dorsal views, left valve, male. Paratype, Io. 602.  $\times 85$ .
- FIGS. 4, 6. External and dorsal views, right valve, female. Paratype, Io. 606.  $\times 85$ .
- FIG. 5. Dorsal view (hinge), left valve, female. Paratype, Io. 605.  $\times 85$ .
- FIG. 12. Dorsal view (hinge), right valve, male. Paratype, Io. 601.  $\times 85$ .

|                                                              |     |
|--------------------------------------------------------------|-----|
| <i>Systemocythere exilofasciata</i> gen. et sp. nov. . . . . | 212 |
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Figs. 7-10, from the Kirton Cementstone Series, Kirton Lindsey.

Figs. 13-17, from the Cave Oolite, South Cave.

- FIGS. 7-10. Right, left, dorsal and ventral views of female carapace. Holotype, Io. 614.  $\times 85$ .
- FIGS. 13, 16. Internal and external views, left valve, male. Paratype, Io. 618.  $\times 85$ .
- FIGS. 14, 15. Dorsal and ventral views of male carapace. Paratype, Io. 615.  $\times 85$ .
- FIG. 17. Muscle scars, right valve, male (slightly retouched). Paratype, Io. 616.  $\times 130$ .



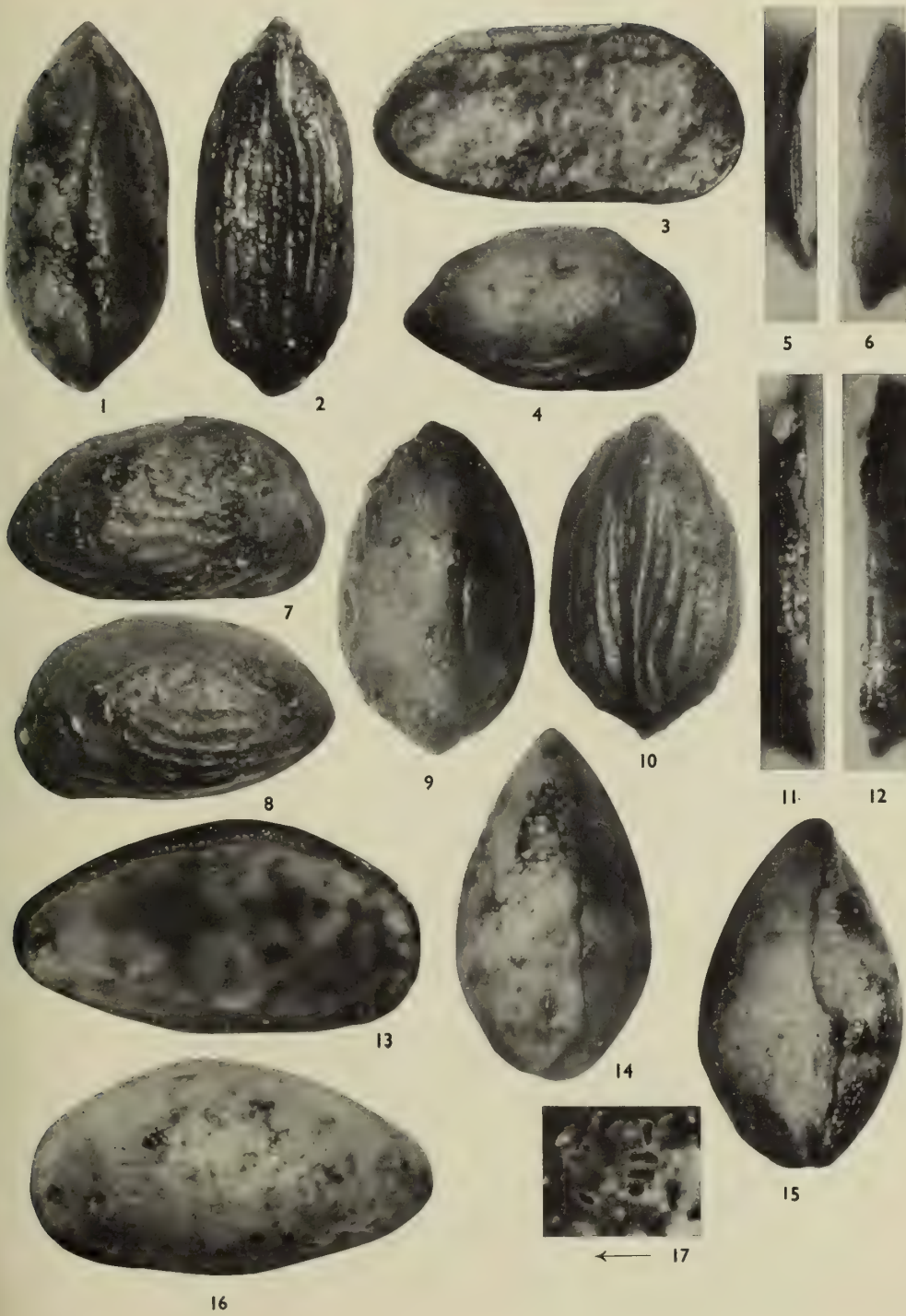














PLATE 15

*Systemocythere exilofasciata* gen. et sp. nov. . . . . page  
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Specimens from the Cave Oolite, South Cave.

FIGS. 1, 2, 4. External views (Fig. 2, showing muscle scars) and dorsal view of right valve, male. Paratype, Io. 619.  $\times 85$ .

FIG. 3. Dorsal view (hinge), left valve, male. Paratype, Io. 618.  $\times 85$ .

*Ektyphocythere triangula* (Brand) . . . . . 214

Figs. 5-15, 17, from the Kirton Shale, Kirton Lindsey.

Fig. 16, from the Cave Oolite, South Cave.

Fig. 18, from the Kirton Cementstone Series, Kirton Lindsey.

FIG. 5. Right valve, exterior. Io. 623.  $\times 85$ .

FIG. 6. Left valve, exterior. Specimen lost, but note smooth anterior half of valve and the presence of the muscle scars as upraised "spots".  $\times 85$ .

FIGS. 7, 12, 15, 17. Right, left, ventral and dorsal views of complete carapace. Io. 627.  $\times 85$ .

FIGS. 8, 9. Dorsal and ventral views of large, adult carapace. Io. 622.  $\times 85$ .

FIGS. 10, 13. Dorsal and internal views, left valve. Io. 626.  $\times 85$ .

FIGS. 11, 14. Dorsal and internal views, right valve. Io. 625.  $\times 85$ .

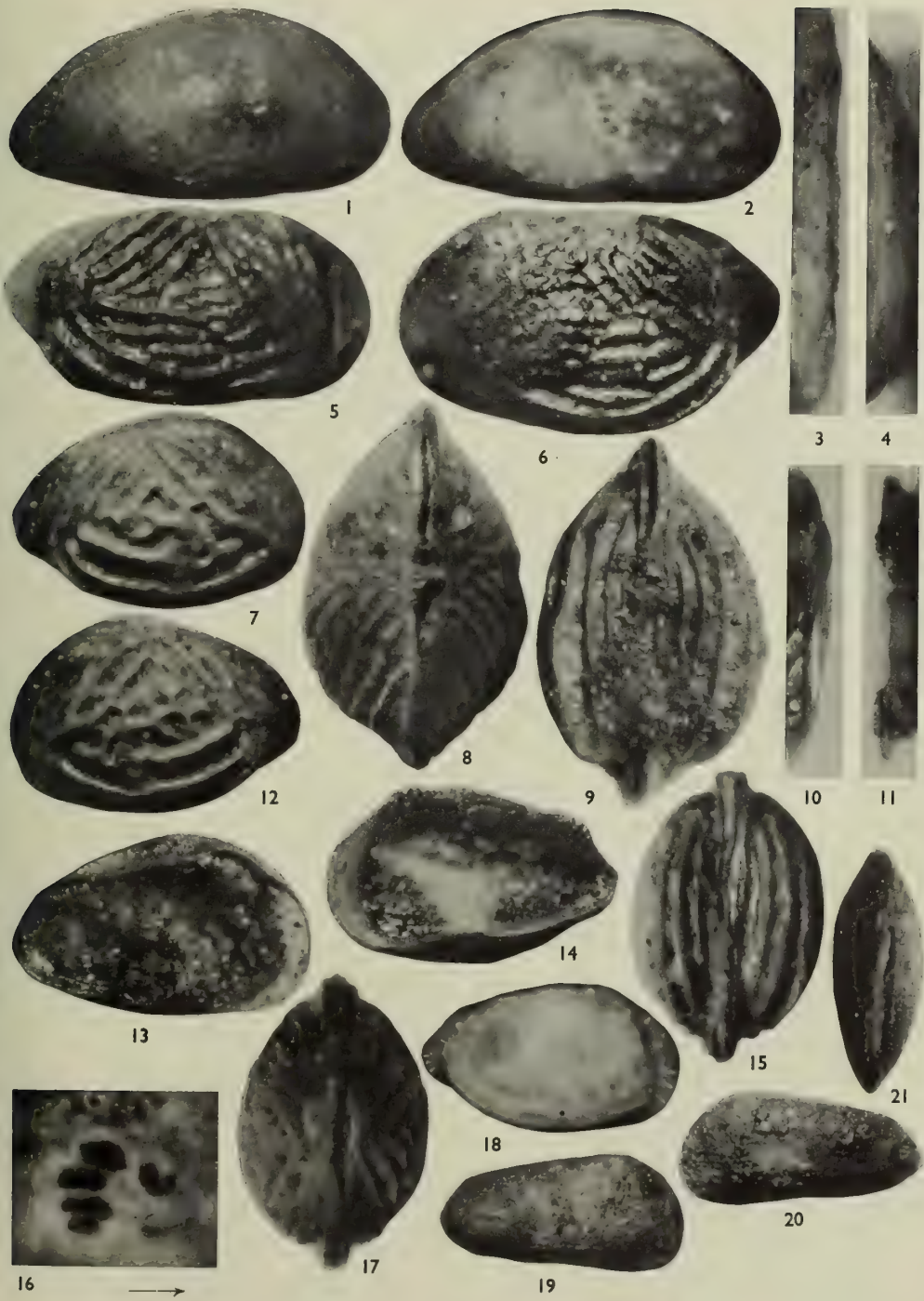
FIG. 16. Muscle scars, left valve. Io. 695.  $\times 190$ .

FIG. 18. Right valve showing radial pore canals. Io. 692.  $\times 85$ .

*Cytheromorpha greetwellensis* sp. nov. . . . . 216

FIGS. 19-21. Right, left and dorsal views of carapace from the Kirton Cementstone Series, Lincoln. Holotype, Io. 620.  $\times 85$ .
















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# THE FAUNA OF THE PORTRANE LIMESTONE

I. THE INARTICULATE BRACHIOPODS

A. D. WRIGHT

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY Vol. 8 No. 5  
LONDON: 1963







# THE FAUNA OF THE PORTRANE LIMESTONE

## I. THE INARTICULATE BRACHIOPODS

BY

ANTHONY DAVID WRIGHT

(Queen's University, Belfast)

*Pp. 221-254 ; 4 Plates ; 5 Text-figures*

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GEOLOGY

Vol. 8 No. 5

LONDON: 1963



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# THE FAUNA OF THE PORTRANE LIMESTONE

## I. THE INARTICULATE BRACHIOPODS

By A. D. WRIGHT

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## SYNOPSIS

This paper is the first of a series by several authors describing a large fauna which has been etched out of the Portrane Limestone. The limestone is of Upper Ordovician age, although the precise horizon has not yet been satisfactorily established. One of the objects of the study is to use the large fauna now available to settle this question. In this part, an introduction to the work is given, followed by a systematic description of the inarticulate brachiopods, covering a total of fifteen genera, including one new genus, *Rowellella*, and eight new species.

## I. INTRODUCTION TO THE PORTRANE LIMESTONE

SITUATED on the coast of Co. Dublin, Eire, about twelve miles north of the capital, is the small but interesting inlier of Portrane, where Lower Palaeozoic rocks are exposed on the eastern edge of a tract of what is dominantly Lower Carboniferous country. Within the rock sequence of the inlier occurs a limestone series, the Portrane Limestone. The present paper is the first of a series of papers describing the fauna of this limestone, or more specifically, of an horizon within the limestone sequence. This horizon has yielded an extraordinary diversity of invertebrate stocks, particularly of brachiopods and arthropods. The exceptionally large fauna will, it is hoped, settle finally the problem of the exact age of the Portrane Limestone within the Upper Ordovician. It is also expected that this fauna will contribute towards the correlation of the Upper Ordovician rocks not only within the British Isles, but also with those of Eastern North America and Scandinavia whose faunas are already known to have affinities with those of Britain.

Due to the large size of the brachiopod fauna it has been necessary to divide it into the two classes. This first part of the study is concerned with the inarticulate brachiopods; the description of the articulate forms will follow in due course. The arthropods, which also form a major part of the fauna, will be described by Dr. W. T. Dean of the British Museum (Class Trilobita) and Dr. Gunnar Henningsmoen of the Paleontologisk Museum, Oslo (Class Ostracoda); I am very pleased to have their co-operation in this project. These two groups will form separate parts of the series.

In the final part, a complete faunal list will include the various other phyla as well as the brachiopods and arthropods, which are present either in a poor state of preservation or else in quantities which are too small to justify the publication of a separate *Bulletin*. In this part also will be included a summary of the conclusions as to the dating of this horizon, which will combine all the faunal evidence available.

## II. HISTORICAL SUMMARY

A description of the geology of the inlier was first given by Medlicott (1853), in which he listed the sixteen fossil species previously recorded by M'Coy (1846) as coming from Portrane. Du Noyer, of the Irish Geological Survey, gave a description of the area (Du Noyer, 1861: 11, 12) which also included a list of some fifty species identified by Baily. This list was revised later (Baily, 1880: 82) and in the revised form was included by Sollas (1895: 101) in his account of the geology of Dublin and its neighbourhood.

The area was remapped by Gardiner & Reynolds (1897) who gave the first precise data on the fossil horizons and localities. The faunas of their principal fossiliferous



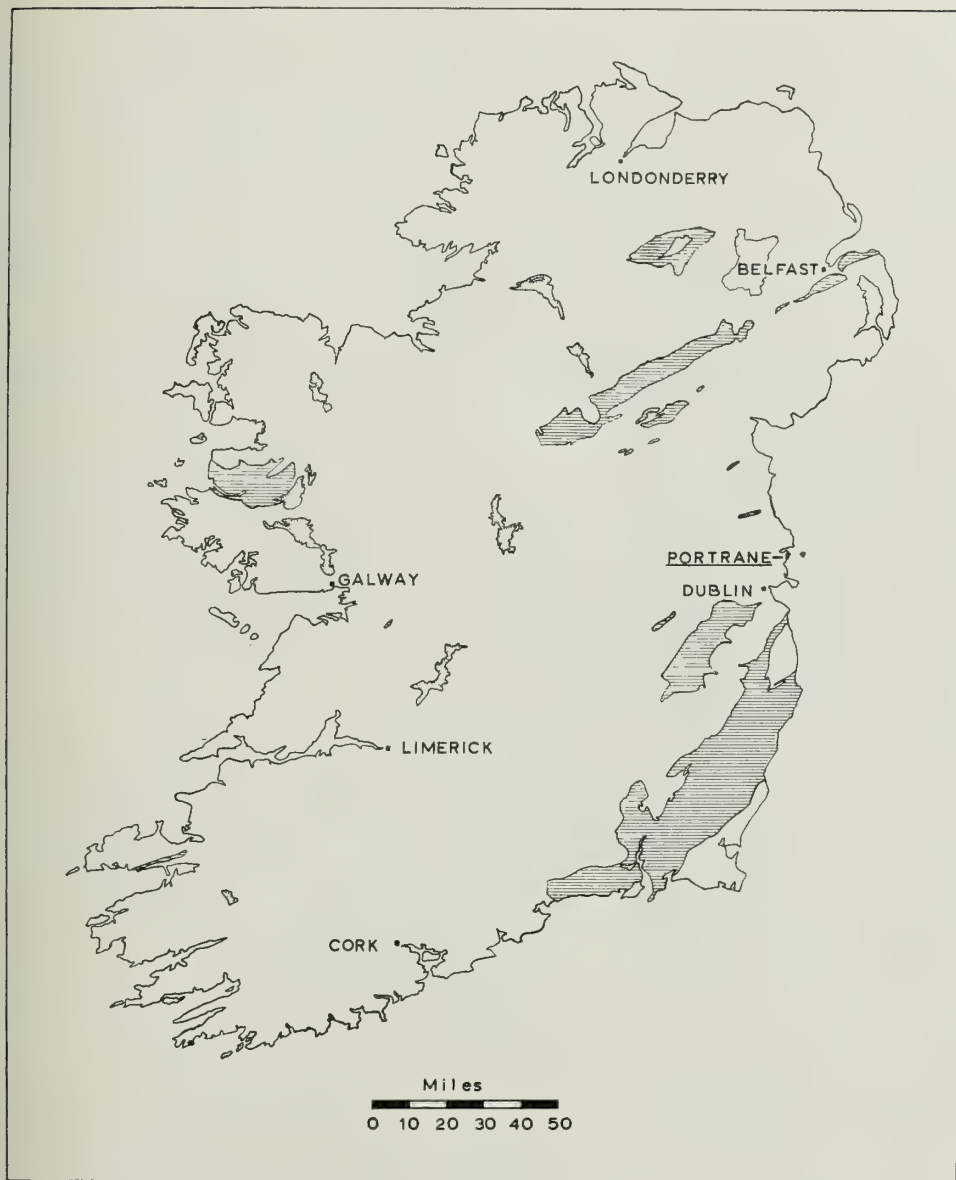


FIG. 1. Map of Ireland to show the situation of the Portrane Inlier relative to the other outcrops of Ordovician rocks (shaded).

horizons were described by Reed in the appendix to this paper. Their largest fauna was obtained from the massive limestone, which, as stated by Harper (1948 : 57), is in the middle of the limestone sequence, with thinly bedded limestones and shales



both above and below. At the time of their investigation a small quarry had just been opened in the massive limestone at the top of a cliff (Gardiner & Reynolds, 1897 : 529, pl. 43, locality "C"), and it was this quarry which yielded to them nineteen trilobites, one ostracod and nine brachiopod species. In commenting on the fauna Reed (1897 : 537) noted that the brachiopods "on the whole seem to be far from common". For the limestone bands below the massive limestone the fauna, according to Reed, consists dominantly of poorly preserved corals, only one trilobite being included in his list (p. 538).

The paucity of brachiopods in Reed's list is surprising, particularly as Baily records the presence of sixteen species of this phylum, and Cole (1892 : 34) says "here at Portrane brachiopod life is at once seen to be abundant".

Since 1897 contributions on the structure of the inlier have been made by Lamont (1938), Shackleton & Harper (1940), whilst Professor J. C. Brindley and Mr. B. Connor of University College, Dublin are currently investigating this aspect of the geology.

Contributions on the age of the limestone have been made by Lamont (1938 : 9 ; 1941 : 455), Stubblefield (1939 : 61), the various opinions being summarised by Harper (1948 : 57). These interpretations of the age of the limestone vary between late Caradocian to early Ashgillian. More recently Dean (1961 : 124) has suggested the possibility of a Puschian age for the Portrane Limestone. The suggested ages have, however, been based principally on one or two trilobite species, rather than an assemblage ; with the large and varied assemblage now available it is hoped to provide conclusive evidence of its age.

### III. THE FAUNA—PRESERVATION AND LOCATION

One feature that has been noted by all who have commented on the Portrane Limestone is that the thinly bedded limestones under the massive limestone contain abundant corals which have been weathered out by the sea. Before the turn of the century it was realised that this occurred because the corals (and the other fossils) had been silicified (Cole, 1892 : 33 ; Sollas, 1895 : 101), but until the current investigation no use of this knowledge had been made to try to obtain a fauna, although etching techniques have now been in use for some years.

The limestone from which the present fauna has been etched is found in this series of thinly bedded limestones and shales, that is, the one beneath the massive limestone. The localities which have proved so profitable are to be found on either side of a small bay immediately to the south-west of the old lime kiln (see Text-fig. 2). At the top of the cliff on the north-east side of the bay is the base of the massive grey limestone ; beneath it are thinly bedded dark limestone bands (about 7 cm. thick) which alternate with black shales. The limestones of this part of the sequence are usually devoid of fossils, and the beds (about  $5\frac{1}{2}$  metres in thickness) show considerable contortion. Beneath these is a band of dark limestone attaining a maximum thickness of 35 cm. This is the highest of the richly fossiliferous horizons from which material was etched, being fossiliferous for a distance of over 10 metres laterally along the cliff. Underlying this are a further 60 cm. of the thin bedded limestone-shale alternations, and then  $1\frac{1}{2}$  metres of highly fossiliferous



limestone, the bands varying from 5 to 23 cm. in thickness, and separated by thin shaly partings; these limestone bands yielded the bulk of the fauna at this locality.

The same horizon can be traced on the south-west side of the bay where it has also yielded a large fauna; further along the coast to the south-west more material has been obtained from this horizon, but here it is by no means so rich in fossils.

The etching of the material was carried out using dilute acetic acid in preference

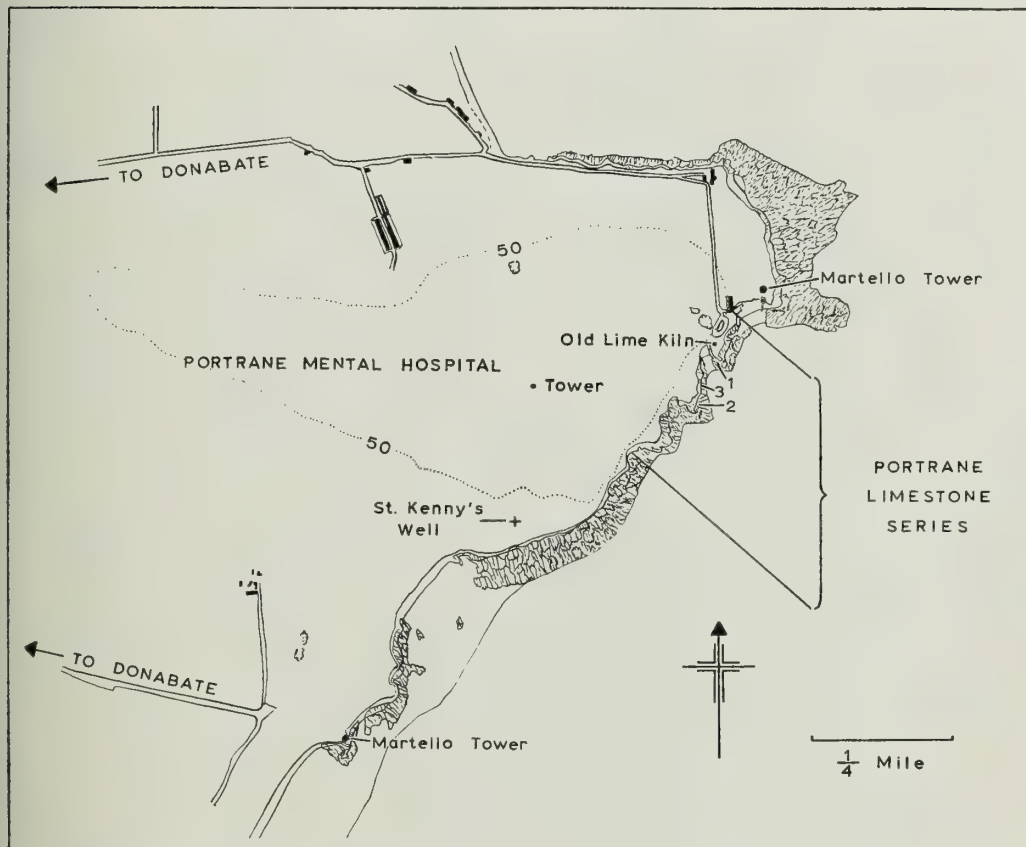


FIG. 2. Sketch-map of the coastline at Portrane, showing the three most fossiliferous localities of the Limestone series. Apart from the continuous outcrop indicated, smaller outcrops occur immediately east of the north Martello Tower, and at the edges of the strand south-west of St. Kenny's Well.

to hydrochloric acid (Bell, 1948) as the latter would have been harmful to the inarticulate brachiopods. Although the etching was consequently a much slower process, the fact, that fifteen genera of these interesting little shells have been recovered more than compensates for the additional time involved.

The actual silicification itself presents problems; in the first place the silicification



is not always complete, so that some specimens are lost or badly eaten away during etching ; secondly the coarseness of the silicification is also variable. The corals, as already stated by Reed (1897 : 538), are in a very inferior state of preservation as a result of the imperfect silicification ; preservation of the brachiopods varies,

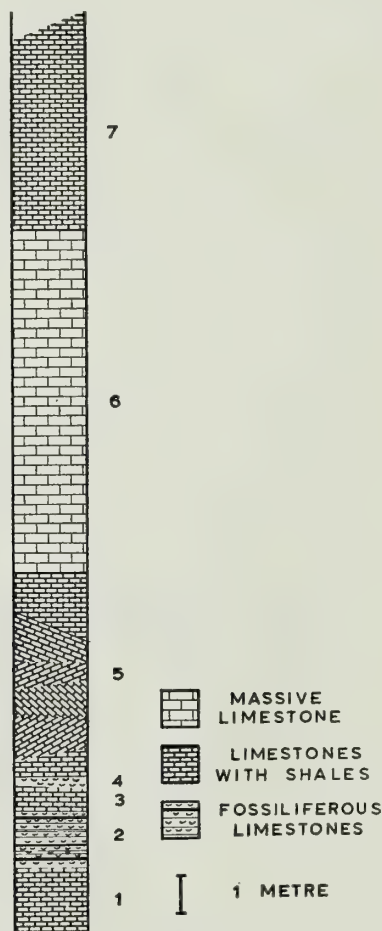


FIG. 3. The Upper Ordovician Limestone sequence of the Portrane Inlier : (1) the lowest thinly-bedded limestone—shale sequence in Lime Kiln Bay, base not seen ; (2) highly fossiliferous limestone bands with thin shale partings ; (3) unfossiliferous limestone and shales ; (4) the highest and thickest limestone band from which a fauna was etched ; (5) highly contorted thinly bedded limestones and shales, very poorly fossiliferous ; (6) pale massive limestone ; (7) upper thinly bedded limestones and shales, an unknown thickness being cut out by faulting.

sometimes they show large coarse rings of beekite, sometimes they are preserved down to the finest details.

The stratigraphy of the inlier as a whole is being investigated by the writer and



will be described elsewhere ; this present series of papers is concerned with the description of the first silicified Upper Ordovician fauna recorded from the British Isles.

#### IV. THE INARTICULATE BRACHIOPODS

Fifteen genera of inarticulate brachiopods are described in the following systematic account and include one new genus and eight new species. Other specimens, which evidently do not belong to any known species, are only represented either as an odd valve or broken fragments. The erection of new species for these forms is not justified on the present material. Certain other etched fragments are too fragmentary for identification or description ; this is the case with "lingulid" fragments in particular. Accordingly these scraps have been retained by the writer pending further material of a more complete nature being recovered from future etchings.

The inarticulates have little to contribute towards establishing the horizon of the limestone, due to the fact that Upper Ordovician forms from other regions are insufficiently known and close comparisons cannot be made. Large scale acetic acid etching has been used on silicified limestones of Cambrian and Middle Ordovician ages (Palmer, 1955 ; Cooper, 1956) ; but not on Upper Ordovician rocks prior to the present investigation.

Of the genera present at Portrane, the only known species of the new genus *Rowellella* is from the Portrane Limestone itself. *Lingulella* is ubiquitous, whilst the genera *Paterula*, *Multispinula*, *Orbiculoidea*, *Schizotreta* and *Trematis* are widespread, being recorded from the British Isles, Europe, America and in some cases North Africa. *Paterula* is generally a rather rare form. The occurrence of *Multispinula* is probably rather high for this genus, which was erected by Rowell (1962) to embrace Middle Ordovician species previously referred to *Schizambon*. Reed (1917) has however recorded the genus from the Drummuck Group (Starfish Bed) at Girvan.

Six genera, previously unknown outside North America, occur at Portrane :—*Leptobolus*, *Acanthambonia*, *Eoconulus*, *Spondylotreta*, *Ephippelasma* and *Scapheasma*. Whilst *Leptobolus* ranges from Trenton to Cincinnati, the remainder are Middle Ordovician forms and all occur in the Pratt Ferry Formation of Alabama, the last two not being recorded outside this particular horizon. Cooper (1956) also obtained a large and varied etched inarticulate fauna, but this should not be taken as indicating close stratigraphical relationship between the Pratt Ferry and the Portrane fauna. It does, however, serve to impress the fact that many inarticulates, which might prove to be useful stratigraphically if sufficient of them could be obtained, must be present in other Ordovician limestones.

Whilst *Spondylotreta* has not previously been recorded from Europe, it may well be that specimens at present masquerading under the names of *Conotreta* and *Acrotreta* actually belong to Cooper's genus.

Of the two remaining genera, *Acanthocrania* and *Philhedrella*, neither has been recorded from the British Isles. The former has a very long range in North America, and occurs in the Estonian Ordovician. *Philhedrella* has apparently been found only in eastern Europe, in the Baltic Ordovician and in the Polish Silurian ; unfor-



tunately there is some uncertainty about this genus as the type species is inadequately known.

The only inarticulate species from Portrane which is undoubtedly conspecific with a described form is *Orbiculoidea shallochensis* Reed, known from the Whitehouse Group at Girvan.

In conclusion, I should like to express my thanks to Dr. A. J. Rowell of Nottingham University for reading and constructively criticising the manuscript, and also to Professor A. Williams for granting me access to his data on the Girvan brachiopods, which had not been published by the time this work was completed.

## V. SYSTEMATIC DESCRIPTIONS

### Superfamily **OBOLACEA** King

### Family **OBOLIDAE** King

### Subfamily **LINGULELLINAE** Schuchert

### Genus **LINGULELLA** Salter, 1866

#### *Lingulella* sp. 1

(Pl. 1, figs. 1-4)

**DESCRIPTION.** The two dorsal valves here placed are small for the genus, and of narrowly oval outline, tapering sharply both anteriorly and posteriorly. Profile gently and evenly convex with maximum width (almost two-thirds of the valve length) at about mid-valve. Ornament of concentric growth lines of variable strength, rather poorly preserved.

Interior with a small apical plate; muscle field about a quarter of the valve length, slightly thickened and of roundedly triangular outline with its front edge convex anteriorly. Differentiation of the muscle field not pronounced. Valve floor anterior to the muscle field traversed by fine, radiating pallial impressions.

**DIMENSIONS.** BB. 28219: length 2.7 mm., width 1.4 mm. BB. 28220: width 1.4 mm.

#### *Lingulella* sp. 2

(Pl. 1, figs. 5, 6)

One dorsal valve and some fragments of this genus resemble *Lingulella* sp. 1 in outline and in the poorly preserved nature of the ornament, the fine concentric growth lines only being clearly seen on one fragment. The complete valve is slightly deeper than in *Lingulella* sp. 1, but the main difference is seen in the muscle field. This is thicker, with the anterior edge straight, and is further divided longitudinally into three sectors, with the median sector depressed below the lateral ones. The presence of a weak median ridge on the valve floor anterior to the muscle field also differentiates the two species. Width of dorsal valve (BB. 28221) 1.1 mm.



*Lingulella* sp. 3

(Pl. 1, figs. 7, 13)

The posterior fragment of a ventral valve (BB. 28222) much larger than the above species shows a pair of well-defined propareas divided by a pedicle groove. The muscle impressions on the valve floor are very faint and show no thickening; the anterior edge of the field appears to be quite straight. Ornament poorly preserved, but one side of the valve shows fine growth lines with a coarser concentric line developed at regular intervals.

DISCUSSION. From the above descriptions, it will be quite clear that species 1 and 2 are quite distinct; the problem is whether sp. 3, represented by a ventral valve, is conspecific with sp. 1. At first sight, the regular development of the stronger concentric lines in sp. 3 appears quite distinctive from that of sp. 1. However, Cooper (1956: 206) describes a species from the "Ottosee formation" of Virginia, *Lingulella virginensis*, which possesses a similar ornament to *Lingulella* sp. 3. Cooper's figured specimen (pl. 1, C, figs. 4, 5) shows, as stated in his plate description (p. 1025), a difference in the ornamentation of each valve. That of the ventral valve is similar to *Lingulella* sp. 3 and that of the dorsal similar to *Lingulella* sp. 1.

Accordingly it may well be that the specimen here referred to as *Lingulella* sp. 3 is in fact the ventral fragment of a large specimen of species 1 or even species 2, the ornament of the latter being too badly preserved to justify a decision either way.

Other fragments of "lingulids" have been recovered from the etchings but in the absence of a distinctive ornament and the all important posterior margin, it is quite impossible to place such fragments in the correct subfamily, let alone genus or species.

## Subfamily ACANTHAMBONIINAE Cooper

## Genus ACANTHAMBONIA Cooper, 1956

*Acanthambonia portranensis* sp. nov.

(Pl. 1, figs. 29-31)

DIAGNOSIS. Ventral valve of subcircular outline, evenly convex in transverse profile; longitudinal profile strongly convex posteriorly, only gently so anteriorly. Shallow but distinct sulcus developed. Surface, including posterior margin, covered with fine hair-like spines and faint concentric growth lines. Beak small; propareas narrow, separated by small pedicle groove thickened into a shallow plate internally at the apex.

Muscle scars not well defined posteriorly, but two very clear sub-oval adductor scars (0.3 mm. long in holotype) situated at about mid-valve; at antero-median extremity of each, and protruding slightly towards mid-valve, is a tiny scar which forms an apparently separate part of the muscle field.

Dorsal valve gently convex; inner surface with two narrow submedian grooves, diverging slightly and extending to margin. Posteriorly these grooves (*vascula*



*media?*) are flanked by poorly-defined muscle fields, present as depressed areas and traversed by further radial grooves.

HOLOTYPE. Ventral valve (BB. 29860) : 1.5 mm. long, 1.7 mm. wide.

PARATYPES. Ventral valve (BB. 29861) : 1.2 mm. long, 1.3 mm. wide. Two broken valves, one ventral (BB. 29862) and the other dorsal (BB. 29863).

DISCUSSION. The new species differs from the two Porterfield species of Cooper, *A. minutissima* and *A. virginensis*, in having a ventral instead of dorsal sulcus ; and in having clearly impressed ventral adductor scars. Although the dorsal valve here described is incomplete, the impressions of the interior compare closely with those of *A. minutissima* (Cooper, 1956, pl. 18, D, fig. 23).

### Subfamily GLOSSELLINAE Cooper

#### Genus *LEPTOBOLUS* Hall, 1871

#### *Leptobolus rarus* sp. nov.

(Pl. 2, figs. 1, 2)

DIAGNOSIS. *Leptobolus* possessing both radial and concentric ornament ; ventral interior with strong ridge extending anterior to pedicle groove, branching as a " U " fork. Two submedian round muscle pits developed anterior to main lateral scars.

HOLOTYPE. Incomplete ventral valve (BB. 28229), 1.3 mm. long.

DESCRIPTION. Ventral valve small, gently convex, of sub-oval outline. Ornament not seen umbonally, anteriorly consisting of fine concentric growth lines, with stronger ones at intervals; and lightly impressed radial ribs. Very fine radiating lines superimposed over the whole surface. Interior with well developed propareas and a moderately deeply impressed pedicle groove, from which the stout internal median ridge extends anteriorly. This thick ridge terminates at about half the length of the muscle field, a pair of finer ridges developing from its outer sides. These diverge slightly and enclose a sub-oval median muscle scar, and then are deflected laterally to form the anterior margin of the main muscle area. Anterior to the point of deflection a pair of smaller rounded pits are developed between the ridges and the median scar. Anterior to the muscle scars, the punctate nature of the inner surface is clearly seen ; two radial ridges on one side of the valve are attributed to vascular origins.

Dorsal valve unknown.

DISCUSSION. This genus was previously unknown in Europe, occurring only in North America, principally in rocks of Trenton-Cincinnatian age (see Foerste, 1924 : 107), although Ruedemann (1901 : 569) records an older species from the Normanskill Shale. This is a black graptolitic shale which contains only two other brachiopods, *Paterula* and *Schizotreta*, both of which are present at Portrane. Cooper (1956 : 214) also records two species from the Edinburg Formation that may probably be referred to *Leptobolus*.

The Portrane form, although only present as a broken ventral valve, is considered to be sufficiently distinctive to warrant the erection of a new species. The only



other species possessing a radial ornament is *L. insignis* Hall, but this lacks the strong ridge in front of the pedicle groove, has a "V" shaped fork, and does not show the small, round and deeply impressed muscle pits anterior to the main scars as in *Leptobolus rarus*.

Genus **ROWELLELLA** nov.

DIAGNOSIS. Small, dorsi-biconvex, elongate sub-rectangular shells with minute marginal beaks. Direction of shell growth alters after young stages so that shell increments are added laterally at right angles to original growth direction, deepening the valve and giving a geniculate appearance to sides of valves in transverse profile. Growth of dorsal valve depressed ventrally along front margin giving a variably developed geniculation to valve, emphasising its convexity. Ornament of somewhat strong, irregular concentric lamellae.

Ventral interior with median thickening posteriorly. Dorsal interior without apical plate; muscle field only known at its anterior end, where a low median ridge separating the scars joins a stronger transverse "W" shaped ridge bounding the field anteriorly. Two sub-parallel or bowing grooves of *vascula media* extend forward from this ridge.

DISCUSSION. The new genus resembles *Pachyglossella* Cooper (1960:601), [= *Pachyglossa* Cooper, 1956, non. Hodgson, 1843, non Fauvel, 1868] in the convex dorsal valve and similar ornament, but differs in the sub-parallel and geniculated lateral margins, while the strong convexity also separates the genus from other obolids, for example *Lingulella*. The features of the dorsal interior are not well known for *Pachyglossella*, hence a comparison cannot be made with *Rowellella*.

The lack of an apical plate in the dorsal valve suggests that the genus belongs to the Glossellinae rather than the Lingulellinae. Only one young specimen shows the structure of the posterior margin of the dorsal valve, and so there is the possibility that the structure is absent because of the youth of the shell.

Apart from two complete young shells, the specimens of the type species all appear to be dorsal valves, with the posterior region invariably broken. The absence of ventral valves may be due to cementation, but as no scars are seen on the complete valves, it would seem more likely that the ventral valves were simply very thin and accordingly easily destroyed. Very thin shell may also account for the absence of the dorsal posterior; the valves thin out posterior to the ridge at the anterior end of the muscle scars in the broken valves, whilst the shell of the young forms is also very thin compared with the thick shell of later growth stages as seen in the larger fragments.

TYPE SPECIES. *Rowellella minuta* sp. nov.

***Rowellella minuta*** sp. nov.

(Pl. I, figs. 8-12, 14-28)

DIAGNOSIS. Small dorsi-biconvex valves of elongate outline, anterior and posterior margins evenly rounded, lateral margins sub-parallel. Lateral margins deflected



towards opposite valve producing a lateral geniculation, accompanied by ventral deflection of dorsal anterior margin and less pronounced reflection of ventral valve. Ornament of strong concentric lamellae only, densities of 12, 12 and 14 per mm. being taken on three specimens.

Ventral interior shows posterior median thickening. Dorsal interior without apical plate. Muscle scars of posterior region of body unknown; anteriorly a low ridge generally divides muscle field into two areas, but in two specimens ridge depressed medianly, indicating that muscles were probably attached in central region also. The ridge terminates against a thickened transverse "W" shaped ridge bounding muscle field anteriorly. From the two anterior points of the "W", two grooves of *vascula media* extend anteriorly either sub-parallel or bowed slightly outwards. Fine, light grooving at anterior margin indicates presence of *vascula terminalia*.

|            |                                     | <i>Length</i> | <i>Width</i> | <i>Thickness</i> |
|------------|-------------------------------------|---------------|--------------|------------------|
| HOLOTYPE.  | Complete shell (BB. 28223)          | . 1.0 mm.     | 0.45 mm.     | 0.25 mm.         |
| PARATYPES. | Complete shell (BB. 28224)          | . 1.2 mm.     | 0.6 mm.      | 0.25 mm.         |
|            | Incomplete dorsal valve (BB. 28225) | . —           | 0.65 mm.     | —                |
|            | Incomplete dorsal valve (BB. 28226) | . —           | 0.75 mm.     | —                |
|            | Incomplete dorsal valve (BB. 28227) | . —           | 1.15 mm.     | —                |
|            | Incomplete dorsal valve (BB. 28228) | . —           | 1.3 mm.      | —                |

DISCUSSION. Due to the broken nature of the posterior margin, no measurements (width excepted) can be taken on the sample except in the case of the two complete shells. These are young shells, but the older shells are still very small, the maximum width recorded being 1.4 mm., whilst the longest shell (broken posteriorly) measures 1.8 mm. The broken posterior margin also prevents an accurate density for the growth lamellae being given, as there can be no control on the position of measurement. This is very important when giving an accurate statistical assessment of the character, as the lamellae vary according to their position, becoming coarser with the increased size of the shell.

Little is known of the ventral interior, the thickening of the posterior region being observed through the exterior of the shell.

### Superfamily **TRIMERELLACEA** Davidson & King

#### Family **PATERULIDAE** Cooper

#### Genus **PATERULA** Barrande, 1879

Little was known about the interior of this rather rare genus until Cooper (1956 : 236) described some well preserved etched specimens, in particular *P. perfecta* from the Pratt Ferry formation. Some of the Portrane shells are equally well preserved, and enable Cooper's description of the valve interiors to be enlarged upon; unfortunately these shells are exceedingly fragile, to the extent that only one ventral valve possesses the flattened marginal rim in its entirety. Thus it is not possible to obtain length and width measurements for the valves to compare directly with those



of Williams (1962 : 88) for *P. balclatchiensis* (Davidson). Measurements of length and width have been taken on the thickened inner edge of the marginal rim to obtain a statistic for "shell outline"; obviously this does not represent a growth line of the shell, but it does give a certain indication of outline for this material.

In the interior of the ventral valve, the present writer regards the whole thickened area of the valve floor posterior and posterolateral to the central scar as constituting the ventral muscle field. The central scar, which is situated at the anterior end of the two slightly divergent impressed grooves arising just in front of the pedicle groove, is pear-shaped rather than circular, with a definite apex at the anterior end. Posterolateral to the central scar is a pair of rounded pits which in some cases seem to be confluent with the smaller anterolateral pair, all being regarded as seats of muscle attachment. The thickened areas posterolateral to the impressed lines form the bulk of the muscle field, with a pair of impressed scars on the lateral edges, and a pair of umbonal scars at the posterior edge. Encircling the muscle field anteriorly are numerous pallial impressions which radiate outwards across the valve floor.

In the dorsal valve the muscle field is large and bluntly sagittate in outline. Posteriorly the deeply inserted umbonal muscle scars are divisible into two; anterolateral to these another pair of triangular pits occurs at the edge of the muscle field. The anterolateral pallial trunks of Cooper are regarded as being anterolateral extensions of the muscle field; the grooves developing at their edge, and passing on to the valve floor, are certainly pallial sinus impressions. The median tongue of the muscle field shows two pairs of small scars, one situated laterally near the posterior end, the other half way along the tongue. A pair of pallial sinus grooves develops from the median anterior margin of this part of the muscle field.

### *Paterula* cf. *perfecta* Cooper

(Pl. 2, figs. 3-5, 8-10, 13, 16)

1956. *Paterula perfecta* Cooper, p. 238, pl. 18H, figs. 54-56, pl. 24D, figs. 12-23.

DESCRIPTION. Small dorsibiconvex shells; ventral valve very gently convex, about one tenth as deep as long; dorsal valve about one sixth as deep as long, but ranging up to a quarter in larger valves. Outline sub-oval to sub-circular. Umbones of both valves sub-marginal; ornament of fine concentric growth lines. Valve interiors with a peripheral rim and a clearly defined pedicle groove and notch in the ventral valve. Muscle and pallial impressions as described above.

DISCUSSION. The species nearest to the Portrane shells are *Paterula perfecta* Cooper, *P. polita* Cooper and *P. balclatchiensis* (Davidson). Internally, allowing for preservation, the Portrane shell cannot be differentiated from *P. perfecta*; unfortunately the interiors of the other species are not known.

Cooper (1956) distinguishes *P. polita* from *P. perfecta* by its smaller size, more oval outline and less convex profile in both valves, and also by its smaller pedicle opening. Text-fig. 4 is a graph showing valve thickness against length for ventral and dorsal valves from Portrane, together with the paratypes of *P. perfecta* (dorsal and ventral) and *P. polita* (dorsal only).



Although only a solitary reading is available for the American shells, and the measurements are given to the nearest 0.05 mm., the following points are noted :

1. The Portrane valves vary over the size range of both *P. polita* and *P. perfecta*.
2. The dorsal valve of *P. perfecta* paratype has identical measurements with a Portrane valve.

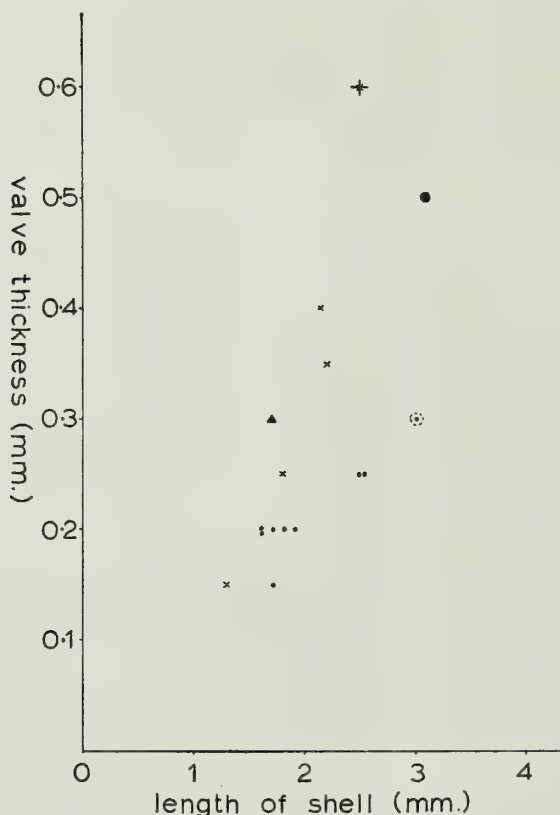


FIG. 4. Graph showing the relationship of valve thickness to length in dorsal and ventral valves of *Paterula*. X—Portrane dorsal valves ; —Portrane ventral valves ; ●—ventral paratype of *P. perfecta* ; +—dorsal paratype of *P. perfecta* ; ▲—dorsal paratype of *P. polita*. The Portrane ventral valve whose length is approximate is enclosed by a broken line.

3. The plots of the Portrane dorsal valves lie on a curve, suggesting allometric growth, with larger valves relatively thicker than smaller ones.
4. The dorsal valve of *P. polita* falls within the scatter of this curve.
5. The gradient for the Portrane ventral valves is very much less than for the dorsal ones, indicating that they are less convex ; a comparison with the solitary valve of *P. perfecta* shows the latter to be much deeper. The Portrane



valve of comparable size is the largest from the locality and is broken anteriorly ; the thickness is 0.3 mm., the length c. 3.0 mm., but may be slightly longer.

From the above it would appear that, first, on actual size, and convexity of the dorsal valve, there is little justification for separating the three forms ; and secondly, the ventral valve is deeper for *P. perfecta* than for the Portrane shells. Unfortunately, the samples are too small to indicate whether this is statistically significant or not.

The width : length ratio for the solitary Portrane ventral valve whose peripheral rim is sufficiently well preserved for measurement, is 80% : measurements on the inner rim for eight valves give ratios of 80, 82, 87, 88, 89, 92, 93, 97%, the mean (and variance) for these figures being 88.5% (31.7). Thus, even using this statistic as indicating outline, there is considerable variation. Measurements taken from Cooper's figures for this statistic give 91, 91, 94, 95, 97%. Comparison by Rank Sum Test shows no significant difference between the two sets of shells.

No figures are available for this statistic for the Balclatchie shells. For the true valve outline Williams (1962) gives 96.4% (var. 35.2) as the ratio for 11 valves ; a direct comparison of this with the " outline statistic " for the Portrane valves by a " T " test shows a significant difference ( $0.01 > p > 0.001$ ) ; whilst such a comparison is not strictly valid it certainly indicates the rounder outline of the Balclatchie shells.

With the evidence available the Portrane shells are placed close to *P. perfecta*, probably differing only in the flatter ventral valve. *P. polita* is very likely also conspecific with *P. perfecta*.

Superfamily **ACROTRETACEA** Schuchert

Family **ACROTRETIDAE** Schuchert

Subfamily **ACROTRETINAE** Schuchert

Genus **SPONDYLOTRETA** Cooper, 1956

This acrotretinid is characterised by the presence of a strong median septum in the ventral valve supporting a spoon-shaped structure at the apex, which in life bears the pedicle. The posterior edges of the structure continue along the inside of the pseudointerarea towards the commissure as a pair of divergent ridges.

Cooper remarks (1956 : 255) that the strong median septum has a similar function to the antero-apical callosity of *Conotreta* ; and indeed it appears rather difficult to distinguish between the two when the median septum of *Spondylotreta* is not so well developed, or when the callosity of *Conotreta* is well developed. This is brought out by figures of an internal cast of *Conotreta davidsoni* (Williams, 1962, pl. 7, figs. 1-3), which show the apex divided into three, indicating an arrangement not very far removed from that of *Spondylotreta*.

Some uncertainty also exists over the dorsal valve of this genus, the ornament being the principal basis for assignment of a solitary concave valve to the type species, *S. concentrica* Cooper.

TYPE SPECIES. *Spondylotreta concentrica* Cooper (1956 : 255).



*Spondylotreta parva* sp. nov.

(Pl. 2, figs. 17, 20-25; Pl. 3, figs. 1, 5, 9, 15)

DIAGNOSIS. Small *Spondylotreta* of sub-circular outline; ornament of fine concentric growth lines continuous across pseudointerarea. Ventral valve conical, with raised median track along pseudointerarea. Dorsal valve flat with shallow median sulcus; dorsal interior with triangular median septum occupying middle half of valve, apex of septum within anterior third of its length; posterolateral muscle field large.

|            |                                   | Length   | Width   | Height     |
|------------|-----------------------------------|----------|---------|------------|
| HOLOTYPE.  | Ventral valve (BB. 29871)         | 1.15 mm. | 1.4 mm. | 1.1 mm.    |
| PARATYPES. | Dorsal valve (BB. 29872)          | 1.3 mm.  | —       | —          |
|            | Dorsal valve (BB. 29873)          | 1.4 mm.  | 1.5 mm. | —          |
|            | Ventral valve (BB. 29874)         | 1.4 mm.  | —       | c. 1.4 mm. |
|            | Unfigured paratypes BB. 29875-76. |          |         |            |

DESCRIPTION. Posterior of conical ventral valve flattened due to the broad pseudointerarea whose elevated median track shows no sign of an intertrough; foramen minute, slightly post-apical. Mean apical angle in longitudinal profile for nine valves was  $79^\circ$  (var.  $74^\circ$ ); for the same valves the mean transverse apical angle was  $87^\circ$  (var.  $95^\circ$ ). The mean height of the cones, measured perpendicularly to the plane of commissure, for seven valves was 75.5% of the valve length (var. 183.6%). The mean ratio of length : width at the commissure for eight valves was 91% (var. 72%).

For the outline of ten dorsal valves a mean length : width ratio of 96.5% (var. 37.4) was recorded, the straighter posterior margin of an otherwise round outline being broken medianly by the small protruding beak. The almost flat profile of this valve is modified by a convex umbonal region and a narrow groove or sulcus developed anteriorly.

The density of the concentric ornament varies according to position of measurement on the shell (p. 234). However, 30, 31 and 33 concentric ridges per millimetre were recorded for one ventral and two dorsal valves respectively.

In the ventral interior, the median septum is formed from a pair of closely opposed parallel plates on the anterior wall, and extends about half way to the commissure. Apically the plates are high, extending to the middle of the valve to unite with a vertical column extending dorsally from the apex. Two divergent plates develop from this column to form a pedicle chamber in the posterior part of the apex. A pair of apical pits (Palmer, 1955 : 768) is situated on the posterior surface at the ends of the pedicle chamber. On the anterolateral surfaces of each side of the apical structure are three simple pallial sinuses; towards the commissure the interior is covered with fine radial lines which are the *vascula terminalia* produced by branching of the main canals.

In the dorsal interior is a triangular median groove posteriorly, bounded laterally by small concave propareas, the inner edges of which are thickened into ventrally projecting eminences. Around the remainder of the valve is a more or less well



defined flat, slightly thickened marginal band or rim. In front of the posterior groove is a subrectangular depression corresponding to the platform of *Conotreta*. Rising anterolaterally from this is a pair of divergent ridges which form the inner edges of a pair of small but clearly impressed areas, probably for muscle attachment. Anterolateral to these is a pair of larger, shallowly impressed sub-elliptical muscle scars, which are bounded on the inside by a low medianly deflected continuation of the divergent ridges and on the outside by the rim. The strong median septum rises gently from the anterior end of the "platform", reaching a sharp point near its front end, then falling sharply to the valve floor.

The mean length from the umbo to the anterior end of the median septum relative to the valve length for ten specimens was 73.6% (var. 15.6); the mean length from the umbo to the maximum height of the median septum relative to valve length for six specimens was 57.3% (var. 23.9); and the mean length of the valve posterior to the median septum to valve length for nine valves was 23.7% (var. 9.95).

DISCUSSION. The size of these shells is very small; the mean length recorded for eight ventral valves was 1.27 mm. (var. 0.22), and for ten dorsal valves 1.15 mm. (var. 0.33). Considering all features of the shells (numbers, size, outline, ornament, etc.) it is evident that the two valves belong together, a factor which is not always clear when working with etched material. These shells are placed in this genus on the basis of the internal structure of the ventral valves, which is rather variably developed in the species, the septa sometimes only being seen as a dark "Y" in the apex of the valve when held up to the light. The large posterolateral muscle field of the dorsal valves agrees with that figured by Cooper (1956) for his type species, confirming the placing of his dorsal valve with the ventral valves of the genus, and further separating the genus from *Conotreta*.

The new species differs from the type species, *S. concentrica*, in having a pronounced median ridge along the pseudointerarea, less developed septa in the ventral interior (which may be accounted for by the smaller size) and a well developed depression anterior to the posterior median groove of the dorsal interior. The only other species at present referred to this genus is *S. ? declivis* (Willard) whose interior is unknown. Its ventral valve differs from *S. parva* in having a concave posterior slope with a well defined intertrough.

### *Spondylotreta* cf. *parva*

(Pl. 2, figs. 11, 12, 14, 15, 18, 19)

Apart from the small delicate *S. parva*, fragmentary specimens of larger, thicker shells (BB. 29877-81) are also present. A strong median ridge in the ventral fragments appears to have supported a spoon-shaped structure umbonally, as in *S. parva*; the pallial markings are much more pronounced but again show a simple pattern.

The dorsal fragments resemble *S. parva* especially in the disposition of the posterolateral muscle scars, but differ in the generally more transverse outline, together with much wider and more substantial propareas, separated only by a weakly developed median groove. Anterior to this, the platform is a thickened area, whilst



the median septum appears to have its maximum development at its posterior end.

It would appear that many of these features are merely the result of thickening, and are thus large forms of *S. parva*; but a specimen of comparable size to *S. parva* (c. 1.2 mm.) shows the transverse outline (the specimen is broken but a length : width ratio on a growth line is 75%) and the contrasting proparea development.

In view of the fragmentary nature of these shells they are placed as *S. cf. parva*; complete material is necessary before the variation of shell outline can be put in perspective, and the problem would be simplified by the recovery of shells showing continuous size variation between the small *S. parva* and the larger shells (the largest incomplete specimen is over 4.0 mm. long).

Genus **EPHIPPELASMA** Cooper, 1956

***Ehippelasma* ? sp.**

(Pl. 3, figs. 2, 6, 10, 14)

DESCRIPTION. Ventral valve minute, of elongatedly conical profile with the apex curved posteriorly, apical angle about 40°. Foramen circular, minute, situated just posterior to the umbo. Outline of commissure transversely elliptical with straight anterior and posterior margins. Pseudointerarea wide, poorly preserved, concave in profile; very slight tendency for a sulcus on the anterior surface of the shell. Ornament of concentric growth lines; valve interior obliterated. Dorsal valve unknown.

DIMENSIONS. BB. 29882: length 0.55 mm., width 0.8 mm., height 0.6 mm.

DISCUSSION. A solitary ventral valve is quite different from the other acrotretinids here described in its valve profile, concave pseudointerarea, and in the elliptical outline of the commissure. The closest known acrotretinid to this valve is *Ehippelasma minutum* Cooper, whose ventral valve appears to differ only in having a slightly narrower transverse apical angle, and in not having such a narrowly elliptical valve outline, which is a specific character of the Portrane shell.

The genus is characterised by the extravagant development of a saddle-shaped plate in the dorsal valve, whose height is 0.6 mm. in the dorsal paratype of *E. minutum*, a valve itself only 0.6 mm. long. Unfortunately, no comparable dorsal valve was found in the Portrane material to confirm the placing of the ventral valve in this genus.

Genus **SCAPHELASMA** Cooper, 1956

***Scaphelasma* ? sp.**

(Pl. 2, figs. 6, 7)

One small acrotretinid dorsal valve (BB. 29883; length 0.6 mm., width 0.8 mm.) appears to belong to this genus. The ornament differs strikingly from that of other members of the subfamily here described, consisting of fine concentric growth lines posteriorly, which pass sharply into very coarse concentric lamellae anteriorly.

The valve is of transversely elliptical outline, convex umbonally, becoming flat



and developing a shallow median sulcus, with convex rims anterolaterally. Valve interior with a short low median septum occupying the middle third of the valve, rising gently towards its anterior end, where a slightly thickened ridge following the shell outline crosses the valve floor. This ridge encloses a pair of sub-reniform muscle scars at its posterolateral extremities. Propareas small, with tooth-like eminences on either side of a median groove which has a thickened anterior margin forming a tiny "shelf". A hollow on the valve floor separates this from the median septum.

The specimen is placed in the genus *Scaphelasma* on the nature of the ornament, and to a lesser extent on outline, profile and valve interior. The "shelf" is somewhat less prominent than that figured by Cooper for *S. septatum* (1956, pl. 18, J) and the septum much lower; neither does the septum reach the anterior margin. These differences, however, may be accounted for by the much smaller size of the Portrane shell. A comparison with the figured exterior of the type, and only, species of *Scaphelasma* from the Pratt Ferry formation shows that the coarse ornament develops very much earlier in the Portrane shell, at about 0.45 mm. instead of 0.75 mm.

Whilst in such a small valve the generalised features of the interior may equally well indicate a *Conotreta*, no species of *Conotreta* possesses this kind of ornament. The possible exception to this is *Conotreta? concentrica* Cooper whose dorsal valve is not known, but which may represent a new genus in Cooper's opinion (1956: 250).

The dorsal valve of *Rhysotreta* also shows several similarities to the Portrane shell, especially in the ornament, but is quite distinct in the development of its interior.

### Superfamily SIPHONOTRETACEA Kutorga

#### Family SIPHONOTRETIDAE Kutorga

#### Genus *MULTISPINULA* Rowell, 1962

#### *Multispinula* sp. 1

(Pl. 3, figs. 22, 23)

One incomplete ventral valve (BB. 29897) and two shell fragments (BB. 29898) are ascribed to this species.

**DESCRIPTION.** Ventral fragment 1.1 mm. long, evenly convex with a slightly procline pseudointerarea. Foramen 0.7 mm. long, almost triangular with straight sides and a slightly irregular anterior edge; posterior part filled by a concave plate situated below the valve surface. Ornament of simple concentric bands only; no spines observed.

The two shell fragments have an ornament of double rows of concentric spine-bearing lamellae which merge together laterally. The alternating spines have a density of about 7 per millimetre along the lamellae, and attain a length of 0.5 mm.

**DISCUSSION.** The genus *Multispinula* was erected by Rowell (1962: 147) to include forms previously referred to *Schizambon*, but which possess a pseudointerarea



and a regular spinose ornament anteriorly. The fragments under discussion are all regarded as belonging to one species, the lack of spines in the umbonal region and their presence anteriorly being typical of many species (e.g. *M. cuneatum* (Willard)). The double row of lamellae on the spinose fragments is seen to merge into a single row laterally; accordingly the presence of only a single row in the young umbonal stages may be expected, and thus does not conflict with the belief that all fragments belong to the same species. An accurate specific determination from this material is not possible.

***Multispinula* sp. 2**

(Pl. 4, fig. 7)

One fragment of this genus (BB. 29899) is separated from the above species, being characterised by a distinctly punctate surface, well seen on the posterior side where the spines are not developed; by finer, more slender spines (9 per mm.) arranged in single rows; and by the absence of concentric lamellae, the spines arising in concentric rows directly from the shell surface.

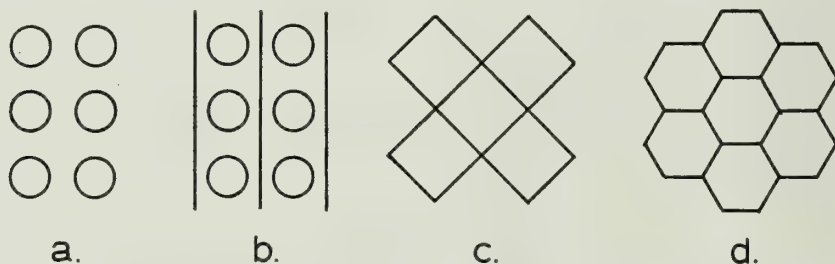


FIG. 5. Diagrammatic representations of the different styles of ornament in the genus *Trematis*: "a"—radial rows of pits; "b"—radial rows of pits separated by radial ribs; "c"—pits arranged in quincunx; "d"—pits arranged hexagonally.

Superfamily **DISCINACEA** Gray

Family **TREMATIDAE** Schuchert

Genus **TREMATIS** Sharpe, 1848

The most distinctive features of this genus are the large pedicle notch of the ventral valve and the unusual ornament. The latter is commonly described as consisting of "small pittings . . . arranged either in quincunx or in radiating rows" (Hall & Clarke, 1892: 139); further distinctions are made on the shape of the pits, and in the second case, on the presence or absence of radial ribs between the rows.

A review of the species ascribed to the genus leads the present writer to the conclusion that there are four basic types of ornament within the genus as understood at present. These are shown diagrammatically in Text-fig. 5. In style "a" the pits are arranged radially but are not separated by ribs as in "b". Style "c" shows a



true quincuncial arrangement, and "d" the commoner hexagonal or honeycomb pattern.

These four basic types do show a certain amount of variation and intergradation. In the Portrane specimens, which are dominantly quincuncial, the pits on part of the shell show a honeycomb pattern. Irregularities of pattern have also been recorded by Wilson (1946 : 23) for the quincuncial *T. terminalis*. Accordingly, it seems doubtful that the quincuncial arrangement seen in *T. parva* will indicate a new genus as suggested by Cooper (1956 : 274), and further, although the majority of species of the genus do not have this pattern, it is developed in the type species (Sharpe, 1848 : 68, Text-figs. 1-3). In Emmons' original figures of *Orbicula terminalis* (1842 : 395, Text-fig. 4) the pits are not shown, only radial ornament being shown on the ventral and only concentric on dorsal valves.

Using the pit arrangements of Text-fig. 5 as a basis, most of the species may be placed in four corresponding morphological groups; for example, style "a" is typical of *T. umbonata* Ulrich, *T. oblata* Ulrich, *T. punctostriata* Hall, *T. corona* Salter; style "b" of *T. siluriana* Davidson, *T. cancellata* (G. B. Sowerby), *T. ottawaensis* Billings, *T. crassipuncta* Ulrich, *T. huronensis* Billings, *T. minneapolis* (Sardeson), *T. foerstei* Cooper; style "c" of *T. parva* Cooper, *T. melliflua* Reed, *T. terminalis* (Emmons), *T. quincuncialis* Miller & Dyer; style "d" of *T. punctata* (J. de C. Sowerby), *T. millepunctata* Hall, *T. craigensis* Reed.

Two of Cooper's species cannot be satisfactorily placed in this grouping. *Trematis? spinosa* is described simply as having "densely crowded pits", which are too fine for the style to be ascertained from the accompanying figures. The species is however quite distinctive in possessing spines. The large, elliptical shaped pits of *T. elliptopora* are irregular and "crudely quincuncial" (Cooper, 1956 : 271) as are the Portrane shells, and so may be classed rather dubiously with style "c".

*T. fragilis* also appears to belong to group "c", for although Ulrich's figured specimen (1889 : 378, fig. 6) is by no means well preserved, it does show a quincuncial arrangement on a posterior fragment of the shell. *T. montrealensis* shows only concentric ornament on the single valve described by Billings (1862 : 52, fig. 57) and accordingly the position of this species is unknown.

### *Trematis* sp.

(Pl. 4, figs. 3, 4, 8)

DESCRIPTION. Minute, subcircular, gently and evenly convex dorsal valves (BB. 29884-85), lacking fold or sulcus. Well developed crudely quincuncial ornament, and occasional well-marked growth stages. In the better of the two specimens, pits are not developed until after the first half millimetre. Anteriorly the ornament shows some variation, a hexagonal pattern replacing the typical quincunx in places. The quincunx may also be lost laterally, where the pits are larger.

Dorsal interior with a thickened posterior margin, divided by a broad median groove. Length of one incomplete dorsal valve (BB. 29884), 1.4 mm.

Ventral valve unknown.



DISCUSSION. In the rather crude quincuncial pit arrangement, especially with the larger, more rounded pits situated laterally, the Portrane shell shows a strong resemblance to *T. elliptopora* Cooper, from the Pratt Ferry formation. The distinctive feature of the latter is that the pits are normally longitudinally elliptical. Those of the Portrane shells are of rather variable outline, but where the pits are elliptical, they differ from those of *T. elliptopora* in being transversely elliptical.

Amongst the British species, *T. corona* Salter occurs in the Cross Fell Corona Beds, and forms close to this have been found in the overlying Dufton Shales as high as the Actonian Stage (Dean, 1959 : 207). In the corresponding stage in Shropshire the genus is represented by *T. punctata* (J. de C. Sowerby) (Dean, 1958 : 223). Neither these, nor *T. craigensis* and *T. siluriana* from the Girvan Ordovician (Reed, 1917 : 818, 819) are close to the Portrane form, as all lack the typical quincuncial arrangement of the pits. Only *T. melliflua* Reed from the Balclatchie mudstones possesses this type of ornament.

Twenty-four pits per millimetre were counted along a line oblique to shell growth on Reed's figure of this species (1917, pl. 4, fig. 10a). For a Portrane valve a count of twenty pits per millimetre was observed, but this attribute certainly varies over the shell surface. Thus as far as can be ascertained the two forms are comparable in density of ornament, but the quincuncial arrangement is far less variable in *T. melliflua*.

The Portrane shell differs further in lacking the pronounced dorsal sulcus and transverse outline of the Balclatchie shell. From the figures of both Reed and of Williams (1962, pl. 7, fig. 22) it may be seen that the sulcus is quite clear at the 1 mm. growth stage, so that the lack of sulcus in the Portrane shells is not a reflection of their much smaller size.

The nature of the Portrane shells shows that they are quite distinct from the other quincuncial species of the genus, but until more complete material is obtained it is considered better to regard these shells as *Trematis* sp.

### Family **DISCINIIDAE** Gray

#### Subfamily **ORBICULOIDEINAE** Schuchert & Le Vene

#### Genus **ORBICULOIDEA** D'Orbigny, 1847

#### *Orbiculoidea shallochensis* Reed

(Pl. 3, figs. 3, 7, 11, 16, 17, 24, 25)

1861. *Discina* (*Orbicula*), small sp., Baily, p. 11.

1880. *Discina*; species undetermined, Baily, p. 82.

1895. *Discina* sp., Sollas, p. 102.

1917. *Orbiculoidea shallochensis* Reed, p. 820, pl. 4, figs. 18-20.

DESCRIPTION. Subcircular, biconical valves. Ornament of fine, even concentric ridges except at the umbones, which are smooth. For the best preserved shell,



counts of these ridges taken over the 1-2 mm. and the 2.5-3.5 mm. positions anterior to the beak, were 16 and 15 per millimetre respectively, showing little increase in thickness of the ridges with shell growth.

Ventral valve with subcentral apex; lateral profile of posterior surface gently convex, and anterior surface gently concave; evenly conical in anterior profile. Pedicle groove broadly lanceolate, extending a quarter of the distance from the apex to the posterior margin, with the small foramen restricted to the posterior extremity.

Dorsal valve initially conical, flattening somewhat later, with the apex one fifth of the length of the valve from the posterior margin. Lateral profile with a flat or slightly concave, relatively steep posterior slope, and a flat, gentler anterior slope; anterior profile a low even cone, flattening laterally.

Ventral interiors of fragments ascribed to this species show the pedicle tube clearly; little is seen in the dorsal interiors except for two faint, slightly divergent raised lines arising at the apex of the valve and continuing anteriorly for a short distance (c. 0.5 mm.).

DIMENSIONS. Dorsal valve (BB. 29887): length 4.4 mm., width 4.6 mm.

DISCUSSION. The Portrane shells agree with Reed's specimens from the Whitehouse Group, Girvan, in all features described by Reed and those evident from his figures (1917, pl. 4, figs. 18-20). The ornament is identical in style and in density (a count anterior to the 1 mm. distance from the apex on Reed's figure 19 gives 15 ridges per millimetre compared with 16 for the Portrane shell; the valve outline and profile are also similar. The dorsal apex is further forward in the figured Whitehouse valve (distance from the posterior margin is 24% of the valve length as opposed to 20% for the Portrane valve) and the pedicle groove is slightly longer in Reed's figure. These differences, however, appear to be well within the limits of normal variation and certainly do not merit separating the two forms, especially on the small quantity of material available for study.

### *Orbiculoidea* sp.

(Pl. 4, figs. 1, 2, 6)

One discinid dorsal valve (BB. 29889) is quite distinct from *O. shallochensis*, differing in the unusual transversely suboval outline. The valve is somewhat broken anteriorly, but measurement on a growth line shows the length to be 65% of the width. The valve (width 4.2 mm.) is quite deep (0.9 mm.), the maximum thickness being just anterior to the apex. The beak itself is directed posteriorly, projecting slightly over the steep, flat, posterior slope. Anterior slope convex; anterior profile evenly convex.

The ornament is even, as in *O. shallochensis*, but slightly coarser (13 ridges per millimetre anterior to the 1 mm. distance from the apex). Interior with a light forked ridge traversing the posterior half from just anterior of the apex to the middle of the posterior margin.



Genus *SCHIZOTRETA* Kutorga, 1848*Schizotreta concava* sp. nov.

(Pl. 4, figs. 5, 9, 10, 12-14)

DIAGNOSIS. *Schizotreta* of sub-circular outline ; ventral valve conical with convex posterior slope ; dorsal valve concave, after short initial convex stage. Dorsal apex close to posterior margin ; ornament of rather coarse, concentric growth ridges which coalesce in posterior part of valve.

HOLOTYPE. Dorsal valve (BB. 29890) 4.6 mm. long.

PARATYPES. Dorsal valve (BB. 29891) : length 1.4 mm., width 1.4 mm. Dorsal valve (BB. 29892) : width 6.1 mm. Other ventral fragments (BB. 29893-95).

DESCRIPTION. Outline subcircular to slightly elongate, young valves circular (3 small valves each have a length : width ratio of 100%). Fragments indicate a highly conical ventral valve with a convex posterior slope ; pedicle groove short, elliptical, listrium grooved medianly. Dorsal valve evenly convex for the first millimetre or so, afterwards flattening and becoming concave. Apex close to the posterior margin, the distance being 15% of the valve length for each of two adult valves, but much less for young valves (e.g. 4, 6, 7%). Apex smooth, an ornament of concentric ridges developing and becoming progressively coarser with increased growth ; between 1 and 2 mm. anterior to the apex, 12, 13, and 14 ridges were counted on three valves ; two valves gave counts of 5, 6 ridges between 3 and 4 mm. in front of the apex. The numerous ridges of the anterior of the shell tend to fuse together in the posterolateral regions to give the relatively small number of thickened ridges between the apex and the posterior margin.

Only the ridge forming the inner side of the pedicle tube is seen in the interiors of the ventral fragments. The tube terminates well inside an unthickened posterior margin.

Dorsal interior with a short lenticular groove situated medianly just inside the posterior margin, slightly anterior to which is a narrow arcuate band, apparently for muscular attachment. This band is about half the valve width, and possesses a pair of deeply inserted muscle pits medianly. In mid-valve, two adductor scars unite antero-medianly to produce a V-shaped scar, posterior to which is a faint ridge. This ridge also appears on the anterior side where it is bounded by the slightly divergent grooves of the *vascula media*. The punctae of the shell substance are clearly seen in the areas away from the muscle scars.

DISCUSSION. The shells of this species are much thickened, and the internal structures obliterated except in one exquisitely preserved young dorsal valve. It is on this valve that the description of the interior is based.

Several of the features of *S. concava* are to be found in other species, but their combination in this species is quite distinctive. *S. conica* Dwight from the Trenton of New York shows similarities in valve profile and in the dorsal interior. It differs in having the dorsal beak much farther forward, which means that there is also no crushing up of the concentric ridges at the posterior border as in *S. concava*. Dwight's comment on the variability, particularly of the ventral profile, in *S. conica* (1880 : 452) also seems pertinent to *S. concava*.



The convex posterior slope seen in the ventral valve of *S. posteroconvexa* Cooper (1956), also characterises the Portrane shell. The features of the dorsal valve of Cooper's species are not known as it based only on two ventral valves, but the ornament is finer and more evenly spaced than in *S. concava*. The Portrane shell is comparable with *S. shuleri* (Willard) in dorsal outline, position of apex, and in a count of 5 ridges per millimetre at 3 mm. from the apex (taken from Cooper, 1956, pl. 21, D, fig. 22) ; Willard's species does not show the concavity typical of the Portrane shell, nor has the ventral valve a convex posterior slope.

*S. willardi* Cooper from the Pratt Ferry formation is undoubtedly the closest known species to the Portrane shell, but not close enough for the possibility of the two being conspecific. Although only fragments of the Portrane ventral valve have been recovered, it would appear to be much more convex than the Pratt Ferry form ; more definite differences are to be seen in the concentric ridges of the dorsal valve, although in outline, profile, and the position of the apex it might be taken for *S. concava*. Whilst the ornament too is of the same general pattern, it is very much finer, 11 ridges being counted over the 3-4 mm. position in one of Cooper's figured dorsal valves, and 10 on another broken valve in about the same position. The concentric ridges also arise much later, the valves being smooth for about 2 mm. distance from the umbo compared with under 1 mm. for the Portrane valves (eight Portrane dorsal valves gave a mean of 0.79 mm. (var. 0.027) for this measurement).

*S. concava* may be differentiated from associated species of *Orbiculoidea* by the coarser ridges, valve profiles, and in the case of *Orbiculoidea* sp., valve outline.

### *Schizotreta* sp.

(Pl. 3, figs. 18-21)

One ventral valve (BB. 29896) is separated from *S. concava* on account of its unusual ornament. There is reason to believe, however, that this is a pathological specimen, and it may possibly belong to *S. concava*.

The shell is broken marginally but is of subcircular outline, with a straighter posterior margin and apex slightly posterior to mid-valve. In profile the posterior slope is convex, and the anterior slope concave as in *S. concava*. The anterior profile is asymmetrically conical (approximate measurements ; length 5, width 3.5 and thickness 3 mm.). The pedicle groove is lanceolate, 1.2 mm. long, and representing about a third of the distance from the umbo to the posterior margin.

The ornament consists of strong, narrow, raised ridges separated by wide flat interspaces so that there are only 3 ridges per millimetre anterior to the 1 mm. distance from the umbo. The interspaces themselves are ornamented by extremely fine ridges or growth lines (5 being counted between two of the larger ridges). Some of these thicken up as they are traced to the anterior, where seven of the stronger ridges were counted per millimetre in the 1-2 mm. position. Converse to normal development, the stronger ridges become closer together towards the margin. A deep cleft on one side of the valve suggests that this is a pathological or, at least, an injured specimen.



Internally, the pedicle tube is clearly seen, and on either side of its continuation into the apex is a pair of deeply impressed almond-shaped adductor scars, aligned between the apex and the posterolateral angles. Two faint, narrowly divergent ridges are directed anteriorly from the apex, lateral to which is another pair of less well defined muscle scars.

Superfamily **CRANIACEA** Forbes

Family **CRANIIDAE** Forbes

Genus **EOCONULUS** Cooper, 1956

***Eoconulus transversus*** sp. nov.

(Pl. 3, figs. 4, 8, 12, 13)

**DIAGNOSIS.** Small, misshapen, cone-shaped chitinous valves, umbones slightly posterior to mid-valve. Outline transverse, length about two-thirds of width. Posterior margin straight, slightly wider than anterior margin, anterolateral and posterolateral extremities rounded. Posterior slope steeper than anterior slope in 5 out of 8 valves; shallow sulcus in anterior slope. Ornament of concentric growth lines, occasionally thrown into strong undulating wrinkles.

Interior with two large sub-reniform adductor scars situated posterolaterally, and extending for half valve length. Short, thickened, tripartite ridge, aligned subparallel to margin sometimes seen posteromedianly.

Ventral valve not known.

|            |           |   |   |   |   |   | Length   | Width    |
|------------|-----------|---|---|---|---|---|----------|----------|
| HOLOTYPE.  | BB. 29900 | . | . | . | . | . | 1.3 mm.  | 1.75 mm. |
| PARATYPES. | BB. 29901 | . | . | . | . | . | 1.3 mm.  | 2.2 mm.  |
|            | BB. 29902 | . | . | . | . | . | 1.55 mm. | 2.3 mm.  |
|            | BB. 29903 | . | . | . | . | . | —        | 1.55 mm. |

**DISCUSSION.** This interesting genus is known only from the dorsal valve; the ventral valve, which was evidently attached, has not been recovered by either Cooper or the present writer. Cooper (1956: 283) obtained specimens from two horizons both older than the Portrane Limestone; from the Botetourt Formation in Virginia and from the Pratt Ferry Limestone of Alabama. The specimens from the former locality are the larger and "differently shaped", but are not good enough for description. The second locality yields the one described species, the type species *E. rectangulatus* Cooper. The size of the Portrane shells is similar to that of the type species, but the differences between the two forms necessitate the erection of a new species for the Portrane shells.

The following statistical data give a comparison of shell shape for the Portrane and Pratt Ferry shells, the dimensions for the latter being taken from Cooper's data.



(a) *Ratio length : width of dorsal valves.*

*E. transversus* sp. n. :—59, 60, 63, 67, 69, 74, 77% ; mean = 67% (var. 47.0).

*E. rectangulatus* Cooper :—66.7, 70, 75, 79, 86% ; mean = 75.4% (var. 56.3).

A Rank Sum Test gives  $p = 0.053$ , indicating that although the Portrane shell is more transverse than the Pratt Ferry shell, the difference is not significant,  $p$  being just over the 5% level.

(b) *Ratio height : width of valves.*

*E. transversus* :—29, 33, 34, 37, 37, 40, 43, 53% ; mean = 38.25% (var. 53.9).

*E. rectangulatus* :—36, 38, 56, 57, 60 ; mean = 49.4% (var. 55.8).

A Rank Sum Test indicates  $p = 0.047$ , thus the relatively low valves of *E. transversus* in transverse profile are significantly different from those of the type species.

(c) *Ratio height : length of valves.*

*E. transversus* :—38, 54, 54, 55, 56, 58, 64% ; mean = 54.1% (var. 62.8).

*E. rectangulatus* :—45, 57, 67, 75, 86% ; mean = 66% (var. 251.0).

On testing, these figures show no significant difference in the longitudinal profile of the two species.

*E. transversus* differs from *E. rectangulatus* in its lower conical transverse profile, and in the presence of a median sulcus on the anterior slope of the shell. Six of the complete valves show an ornament of simple concentric growth lines, but one specimen also has strong undulating wave-like wrinkles. This ornamentation is rather similar to that of *Undiferina* Cooper (1956). However, there is little doubt as to the affinities of this Portrane valve, as another valve shows an intermediate stage between it and the more usual type, showing a few wrinkles developed on part of the shell only. This irregular surface with variable wrinkles is of course typical of many craniaceids.

Genus **ACANTHOCRANIA** Williams, 1943

*Acanthocrania* was erected as a subgenus of *Crania* to include "Cranias with dorsal valves ornamented by fine papillae or fine spines" (J. S. Williams, 1943 : 71). The type species, *C. spiculata*, is a Carboniferous form, but Cooper (1956 : 283) records the genus as being widely distributed and fairly abundant in the Ordovician of North America. Gorjansky (1960 : 177) does not record the genus from the U.S.S.R., but there is no doubt that three Estonian forms [von Huene, 1899, *Philhedra pustulosa* (p. 298), *P. hemipustulosa* (p. 304) and *Craniella papillifera* (p. 317)] may be referred to this genus as at present defined.

Neither the genus nor any craniaceid referable to it, have been previously described from the British Isles. Although the genus is not common at Portrane, there appear to be two distinct forms represented.

TYPE SPECIES. *Crania spiculata* Rowley (1908).



*Acanthocrania cracentis* sp. nov.

(Pl. 4, figs. 22, 25, 26)

DIAGNOSIS. Dorsal valve deep, transversely subcircular with straight posterior margin. Anterior profile asymmetrically convex; lateral profile evenly convex anterior to beak, steep and gently concave posterior to beak. Maximum valve thickness at mid-valve; beak situated posteriorly, curved over towards posterior margin and below greatest height of valve. Ornament of well marked growth lines giving somewhat lamellose appearance, and fine spines (those preserved being up to 0.3 mm. long), exact relation of spines to growth lines being obscured by silicification.

Interior with pair of large rounded anterior adductor scars (length  $\frac{1}{4}$  of the valve length) situated slightly posteriorly to centre of valve and separated by groove along which is a low ridge, extending anteriorly. Posterior adductor scars transversely oval, about half the length of anterior pair, situated in front of posterior submarginal groove, where they are separated by raised median area.

Ventral valve not known.

HOLOTYPE. BB. 29904; length 4.4 mm., width 5.0 mm., thickness 2.1 mm.

DISCUSSION. The distinctive lateral profile, with the umbo situated below the maximum height and the posterior position of the umbo, serve to differentiate the new species from all others except *A. spinosa* Cooper. The Portrane form differs from this species in its much neater form, regular outline, finer spinose ornament and clearer concentric ornament.

*Acanthocrania* sp.

(Pl. 4, figs. 11, 15, 16, 19)

DESCRIPTION. Three incomplete irregular dorsal valves (BB. 29905-07) of sub-rounded outline, gently to strongly convex profile. Apex posterior of mid-valve; posterior slope flat to concave, anterior slope convex. Irregular concentric ornament covered by coarse stout spines 0.5 mm. or more in length. Interior with a pair of large muscle scars situated posteriorly to the centre of the valve, and separated by a smooth groove which develops anteriorly into a ridge. Here it is bounded by two impressed areas which bear vascular markings in the form of radiating ridges. Width of one incomplete dorsal valve (BB. 29905), 8.8 mm.

DISCUSSION. Whilst the incomplete nature of these shells (especially posteriorly) prevents their specific determination, sufficient features are preserved to distinguish them from the associated *A. cracentis*.

The shells differ from *A. cracentis* in possessing a much coarser spinose ornament, a very variable and irregular profile, and a beak which is relatively farther from the posterior margin and which does not overhang the posterior slope. (It should be mentioned that the position of the beak was not established for one valve because of its very coarse silicification).

Internally the groove separating the anterior adductor scars lacks the median ridge of *A. cracentis*, but this does not seem to be a specific character, the variable nature of its occurrence being recorded for *A. pustulosa* by von Huene (1899: 298).



Genus ***PHILHEDRELLA*** Kozlowski, 1929

This genus was erected as a subgenus of *Philhedra* Koken (1889) by Kozlowski (1929 : 40) for those forms closely resembling *Philhedra* but which possess a smooth or concentrically ornamented surface, lacking the radial ornament of *Philhedra* s.s.

*Philhedra* was originally placed in the Gastropoda by Koken (1889 : 465) although he later (1897 : 112) placed it close to the craniaceid brachiopod *Pseudocrania*. This was accepted by von Huene (1899 : 297), who, although he subdivided the species into two groups based on this differing ornamentation, did not rate this character as constituting a basis for further generic distinction. Von Huene considered the large size of the anterior adductor scars relative to that of the posterior adductor scars to be a more important character, this feature differentiating *Philhedra* from *Petrocrania* Raymond 1911 (syn. *Craniella* Oehlert non Schlotheim, 1820).

Kozlowski (1929) sub-divided Koken's genus on the ornamentation, since when the name *Philhedra* has been generally restricted to those shells possessing radial ornament (Maillieux, 1936 : 46 ; Cooper, 1944 : 291 ; Gorjansky, 1960 : 176).

Unfortunately the type species of *Philhedrella*, *P. mimetica*, is very inadequately known, no information being available on either the ventral valve (which is generally thought to be extremely thin or non-existent in the genus (Kozlowski, 1929 : 41 ; Cooper, 1956 : 284)) or the all important dorsal interior. Thus the type species is just as likely, on present evidence, to belong to *Petrocrania* as to the smooth *Philhedra*, *Philhedrella*. Re-investigation of the type species may lead to the suppression of *Philhedrella*, in which case a new name will have to be erected for the forms with a *Philhedra*-like interior but a smooth or concentrically ornamented exterior.

One of the Portrane craniaceid species possesses these characters and is here included in the genus *Philhedrella*, at least until such time as the type species is re-investigated.

TYPE SPECIES. *Philhedrella mimetica* Kozlowski (1929 : 40).

***Philhedrella celtica*** sp. nov.

(Pl. 4, figs. 17, 18, 20, 21, 23, 24)

DIAGNOSIS. Dorsal valve large, sub-conical with long, almost straight posterior margin, whose width approaches maximum valve width. Apex unobtrusive, situated posterior to mid-valve. Interior with large adductor scars, anterior pair larger than posterior pair, which abut upon posterior margin.

HOLOTYPE. BB. 29908. Length about 22 mm.

PARATYPE. BB. 29909. Width about 22 mm.

DESCRIPTION. Large subconical dorsal valve, apex situated posterior to mid-valve. Anterior profile a low cone ; lateral profile with a gently convex anterior slope and flat or gently concave posterior slope, the latter forming a triangular area bounded by the straight, but somewhat irregular, posterior margin. Posterolateral angles sharply obtuse, lateral margins gently convex, the curvature increasing at the antero-lateral angles to form a straight anterior edge medianly. Valve



surface rather uneven, ornamented by fine growth lines and developing irregular concentric wrinkles on large shells.

Dorsal interior with large anterior and smaller posterior pairs of adductor scars, the posterior edge of the latter lying on the valve margin. The former are sub-oval (width about  $\frac{3}{4}$  of the length), swollen and extending almost a third of the valve length in the holotype. They are situated anterolaterally to the valve apex and are well separated by a groove (more than half the width of an individual scar), along which is a low ridge. This broadens anteriorly forming a thickened margin to the scutellum, from which a median ridge (rostrum) and two less well marked antero-lateral ridges project. Posterior adductor scars of subtriangular outline, with the apex directed anterolaterally. Width similar to anterior scars, but only half the length. Smaller muscle scars situated lateral to these, in the posterolateral corners of the shell. The depressed areas on either side of the rostrum show a series of parallel pallial ridges, roughly perpendicular to the margin, which may be traced towards the posterolateral angle.

Ventral valve unknown.

DISCUSSION. The material consists of three sub-conical dorsal valves, together with two other fragmentary specimens. The latter show the same pair of very large swollen anterior adductor scars, one being a very low cone with poor concentric ornament, the other flatly convex. The broken nature of these shells, which are believed to be flattened areas of larger conical valves, prevents their being used in the systematic description of the species.

The Portrane shells are quite distinct from the other Ordovician craniaceids which may belong to this genus. One of these is *Crania trentonensis* Hall, for which figures of the diagnostic dorsal interior are unknown to the writer, but which has been placed in the genus *Petrocrania* by Cooper (1956: 290). Whether this generic assignment is correct or not, the valve outline alone is sufficient to distinguish the species from the Irish form, as it lacks the straight posterior margin of the latter, and also has its greatest width towards the anterior margin (see Hall & Clarke, 1892, pl. 4, H, fig. 21).

Of the Estonian forms which have the features of *Philhedrella*, *P. acra* (von Huene, 1900: 179) resembles the Portrane shell in its development of a steep, triangular posterior surface, but differs in its smaller size, the narrow posterior margin relative to valve width and the clearly defined button-like apex. *P. glabra* has a similar profile, but the outline lacks the long posterior margin of *P. celtica* whilst the interior has small, oval posterior muscle scars, situated well inside the valve margin. The sole specimen of *P. mitrata* again lacks the distinctive outline of the Portrane shell; von Huene's figure is not very clear (1899, pl. 5, fig. 6). *P. bucculenta* differs in its sub-central button-like apex and round outline, whilst *P. despectata* also lacks the straight posterior margin and triangular surface posteriorly.

*P. kokeni*, which ranges up into the Rakvere stage, resembles *P. celtica* in size and general appearance of the exterior, although of a somewhat more subquadrate outline. Internally the differences are very marked, the Estonian form having oval posterior adductor scars situated well away from the margin, and anterior ones which are "bean-shaped" and which converge anteriorly.



No craniaceid species comparable with *P. celtica* are recorded from the British Isles.

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PLATE I

*Lingulella* sp. 1 . . . . . p. 230

FIGS. 1, 2. Interior and exterior of dorsal valve. BB. 28219.  $\times 12$ .

FIGS. 3, 4. Interior and exterior of dorsal valve, broken anteriorly. BB. 28220.  $\times 12$ .

*Lingulella* sp. 2 . . . . . p. 230

FIGS. 5, 6. Interior and exterior of dorsal valve. BB. 28221.  $\times 12.3$  and  $13.2$  respectively.

*Lingulella* sp. 3 . . . . . p. 231

FIGS. 7, 13. Interior and exterior of a broken ventral valve, the latter showing fine growth lines with a stronger concentric line at regular intervals on one side of the shell. BB. 28222.  $\times 8.5$ .

*Rowellella minuta* gen. et sp. nov. . . . . p. 233

FIGS. 8, 14, 15. Anterior, internal and lateral views of incomplete dorsal valve. Paratype, BB. 28226.  $\times 26$ .

FIGS. 9-11, 16. Ventral, dorsal, lateral and posterior views of the holotype, BB. 28223.  $\times 27$ .

FIGS. 12, 17-19. Ventral, posterior, lateral and dorsal views of paratype, BB. 28224.  $\times 27$ .

FIGS. 20, 21, 27, 28. Posterior, anterior, internal and external views of incomplete dorsal valve. Paratype, BB. 28228.  $\times 12$ .

FIGS. 22-24. Lateral, external and internal views of incomplete dorsal valve. Paratype, BB. 28225.  $\times 26$ .

FIGS. 25, 26. External and internal views of incomplete dorsal valve. Paratype, BB. 28227.  $\times 14$ .

*Acanthambonia portranensis* sp. nov. . . . . p. 231

FIG. 29. Interior of dorsal fragment. Paratype, BB. 29863.  $\times 12.5$ .

FIGS. 30, 31. Exterior and interior of ventral valve. Holotype, BB. 29860.  $\times 9.7$ .















## PLATE 2

*Leptobolus rarus* sp. nov. . . . . p. 232

FIGS. 1, 2. Interior and exterior of incomplete ventral valve. Holotype, BB. 28229.  $\times 16.5$ .

*Paterula* cf. *perfecta* Cooper . . . . . p. 235

FIGS. 3, 4, 9, 16. Four fragmentary ventral valves showing the muscle and pallial markings of the valve interior. BB. 29864-67. Figs. 3, 4  $\times 15$ ; Figs. 9, 16  $\times 20$ .

FIG. 5. Interior of a dorsal valve, muscle scars not prominent. BB. 29868.  $\times 11.5$ .

FIG. 8. Interior of an older dorsal valve, muscle field well developed. BB. 29869.  $\times 10.5$ .

FIGS. 10, 13. Internal and external views of an almost complete ventral valve. BB. 29870.  $\times 12$ .

*Scaphelasma?* sp. . . . . p. 240

FIGS. 6, 7. Exterior and interior of dorsal valve. BB. 29883.  $\times 19$ .

*Spondylotreta* cf. *parva* . . . . . p. 239

FIGS. 11, 15. Dorsal fragments showing the features of the interior. BB. 29879, BB. 29880.  $\times 6$ ,  $\times 6.5$  respectively.

FIGS. 12, 14. Ventral umbonal fragments, the former showing pronounced pallial markings. BB. 29877, BB. 29878.  $\times 6$ ,  $\times 11.4$  respectively.

FIGS. 18, 19. Interior and exterior of a damaged dorsal valve. BB. 29881.  $\times 6.3$ .

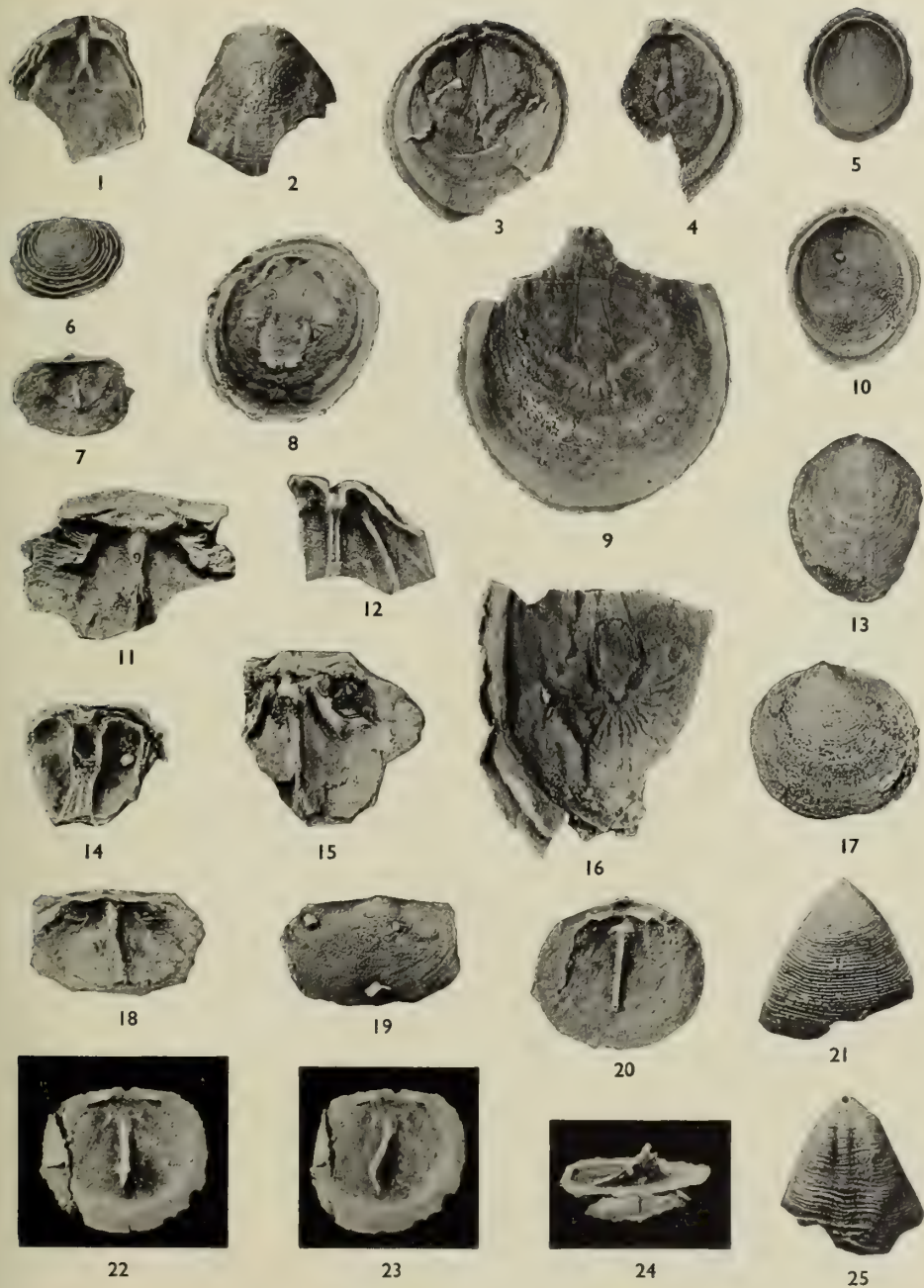
*Spondylotreta parva* sp. nov. . . . . p. 238

FIGS. 17, 20. Exterior and interior of a dorsal valve. Paratype, BB. 29873.  $\times 15.6$ .

FIGS. 21, 25. Lateral and posterior views of a ventral valve, damaged marginally. Paratype, BB. 29874.  $\times 14.6$ .

FIGS. 22-24. Ventral, oblique and lateral views of a damaged dorsal interior to show the muscle scars and strong median septum, this being slightly broken anterior to its apex. Paratype, BB. 29872.  $\times 15.4$ .















# PLATE 3

*Spondylotreta parva* sp. nov. . . . . p. 238

FIGS. 1, 5, 9, 15. Four views of the interior of the ventral valve to show the nature of the apical structures and pallial markings. Holotype, BB. 29871.  $\times 24$ .

*Ephippelasma?* sp. . . . . p. 240

FIGS. 2, 6, 10, 14. Anterior, posterior, apical and lateral views of ventral valve. BB. 29882.  $\times 22.5$ .

*Orbiculoidea shallochensis* Reed . . . . . p. 244

FIGS. 3, 7, 11. Lateral, ventral and dorsal views of incomplete pair of valves. BB. 29886.  $\times 6$ .

FIGS. 16, 17, 25. Interior and exterior of a dorsal valve. BB. 29887.  $\times 3.5$ , and an enlargement of the interior,  $\times 4.8$ .

FIG. 24. Interior of ventral fragment, showing pedicle tube. BB. 29888.  $\times 6.2$ .

*Eocomulus transversus* sp. nov. . . . . p. 248

FIG. 4. Interior of dorsal valve. Holotype, BB. 29900.  $\times 11$ .

FIGS. 8, 12, 13. Antero-dorsal, dorsal and posterior views of a dorsal valve. Paratype, BB. 29901.  $\times 11.7$ .

*Schizotreta* sp. . . . . p. 247

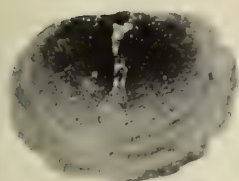
FIGS. 18-21. Lateral, oblique, ventral and internal views of a ventral valve. BB. 29896.  $\times 3.3$ .

*Multispinula* sp. 1 . . . . . p. 241

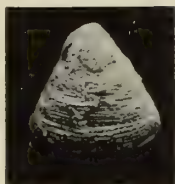
FIG. 22. Incomplete ventral valve showing characteristic foramen. BB. 29897.  $\times 21$ .

FIG. 23. Fragment of anterior part of a valve, showing ornamentation. BB. 29898.  $\times 6.6$ .





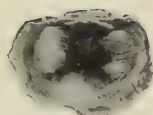
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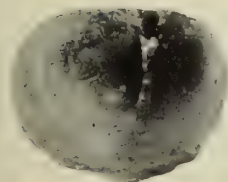
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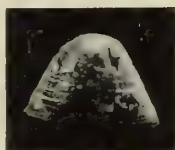
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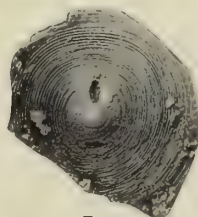
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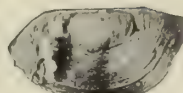
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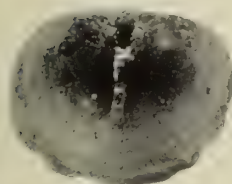
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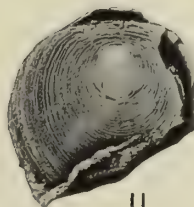
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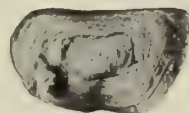
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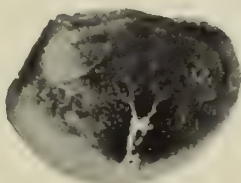
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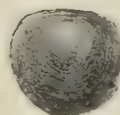
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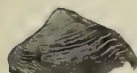
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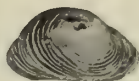
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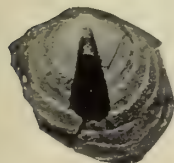
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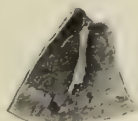
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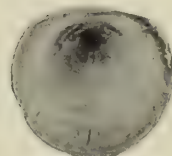
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23



24



25











# PLATE 4

*Orbiculoidea* sp. . . . . p. 245

FIGS. 1, 2, 6. External, lateral and internal views of dorsal valve. BB. 29889.  $\times 6$ .

*Trematis* sp. . . . . p. 243

FIGS. 3, 8. Exterior and interior of incomplete dorsal valve. BB. 29884.  $\times 12.8$ .

FIG. 4. Exterior of a dorsal fragment. BB. 29885.  $\times 13.2$ .

*Schizotreta concava* sp. nov. . . . . p. 246

FIGS. 5, 10, 14. Interior and exterior of a small dorsal valve, BB. 29891,  $\times 10$ , and an enlargement of the interior,  $\times 15$ . Paratype.

FIG. 9. Exterior of dorsal valve. Holotype, BB. 29890.  $\times 3.7$ .

FIG. 12. Exterior of dorsal valve. Paratype, BB. 29892.  $\times 2.7$ .

FIG. 13. Interior of ventral fragment showing pedicle tube. Paratype, BB. 29893.  $\times 3.9$ .

*Multispinula* sp. 2 . . . . . p. 242

FIG. 7. Fragment of a valve showing ornamentation. BB. 29899.  $\times 10.8$ .

*Acanthocrania* sp. . . . . p. 250

FIG. 11. Exterior of broken dorsal valve. BB. 29906.  $\times 2.5$ .

FIGS. 15, 16. Anterior and dorsal views of incomplete dorsal valve. BB. 29905.  $\times 2$ .

FIG. 19. Interior of incomplete dorsal valve. BB. 29907.  $\times 1.9$ .

*Acanthocrania cracentis* sp. nov. . . . . p. 250

FIGS. 22, 25, 26. Internal, lateral and external views of dorsal valve. Holotype, BB. 29904.  $\times 3.4$ .

*Philhedrella celtica* sp. nov. . . . . p. 251

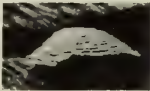
FIGS. 17, 18, 21. Dorsal, lateral and internal views of dorsal valve. Holotype, BB. 29908.  $\times 1.2$ .

FIGS. 20, 23, 24. Internal, lateral and dorsal views of a dorsal valve. Paratype, BB. 29909.  $\times 1.4$ .

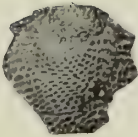




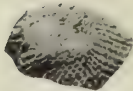
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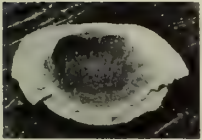
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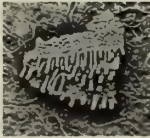
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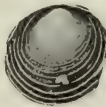
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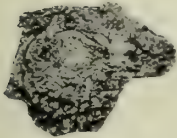
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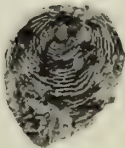
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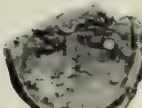
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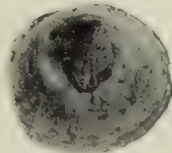
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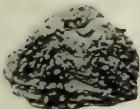
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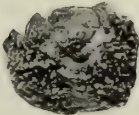
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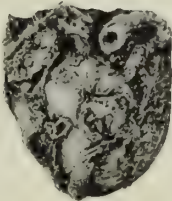
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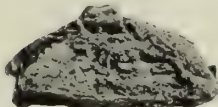
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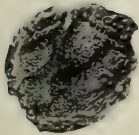
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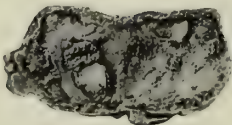
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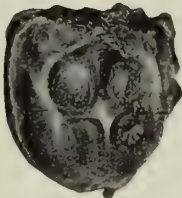
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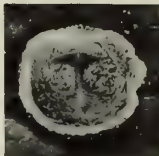
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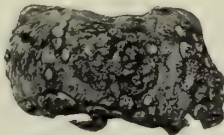
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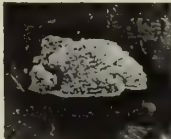
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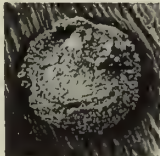
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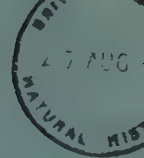




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CERTAIN PALAEONISCOID FISHES  
AND THE EVOLUTION OF THE  
SNOUT IN ACTINOPTERYGIANS



B. G. GÄRDINER

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY

Vol. 8 No. 6

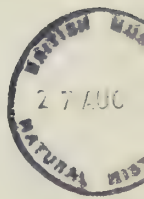
LONDON: 1963







CERTAIN PALAEONISCOID FISHES AND THE  
EVOLUTION OF THE SNOUT IN  
ACTINOPTERYGIANS



BY

BRIAN GEORGE GARDINER, Ph. D.  
(Queen Elizabeth College, University of London)

*Pp. 255-325; 2 Plates; 20 Text-figures*

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# CERTAIN PALAEONISCOID FISHES AND THE EVOLUTION OF THE SNOOT IN ACTINOPTERYGIANS

By B. G. GARDINER

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## SYNOPSIS

A redescription is given of the type species of the genera *Watsonichthys* Aldinger, *Cosmoptychius* Traquair, *Nematoptychius* Traquair and *Mesonichthys* *gen. nov.* from the British Carboniferous, supplemented by an account of members of the Devonian genera *Stegotrachelus* Woodward and White, *Moythomasia* Gross, *Tegeolepis* Miller and *Cheirolepis* Agassiz, and the Permian *Rhabdolepis* Troschel and *Amblypterus* Agassiz. These genera are placed in appropriate families, and the evolution of the snout region in actinopterygians is discussed.

## I. INTRODUCTION

THE British Carboniferous strata have yielded a vast array of palaeoniscoids. A few of these, nine in all, were described by Agassiz as long ago as 1843, but the main contribution to our knowledge of these forms was given by Traquair (1877-1914) in his monograph on "The Ganoid fishes of the British Carboniferous formations". More recently Moy-Thomas and Dyne (1938) have redescribed the Lower Carboniferous palaeoniscoid fauna from Glencartholm, Eskdale, in an attempt to supplement those descriptions already given by Traquair (1877-1914). Apart from these accounts, the only other real contribution has come from White (1927, 1937 and 1939) who has described several new Carboniferous genera.

This paper is intended to be the beginning of a revision of all the genera described by Traquair (1877-1914) with the exclusion of those genera adequately redefined by Moy-Thomas & Dyne (1938). This work is mainly concerned with redefining selected genera, and to that end only the type species are dealt with. In subsequent papers it is hoped to redefine the remaining Carboniferous genera, and then to examine the vast array of species which have been included within them. This is only possible when adequate generic descriptions are available. Needless to say, any such study is supplemented by digressions on the part of the writer into descriptions of genera other than Carboniferous where they are of interest to him and to the evolutionary picture as a whole. Thus I have redescribed several Devonian and two essentially Permian genera.

Some attempt is made at classification into families, although their relationships to one another are not dealt with exhaustively at this stage.

In the course of this work the problem of the snout region in the palaeoniscoids has become somewhat clearer and the main contribution made in the discussion is an effort to elucidate the evolution of the actinopterygian snout.

The following letters indicate some of the Museums from which specimens were borrowed :—

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- B.M.N.H. British Museum (Natural History), London.
- R.S.M. The Royal Scottish Museum, Edinburgh.
- U.M.Z.C. University Museum of Zoology, Cambridge.



## II. SYSTEMATIC DESCRIPTIONS

Order **PALAEONISCIFORMES**Sub-order **PALAEONISCOIDEI**Family **ELONICHTHYIDAE** Aldinger, 1937 : 16

DIAGNOSIS. See Aldinger, 1937 : 16, 204.

Genus **ELONICHTHYS** Giebel, 1848

DIAGNOSIS (emended). Body fusiform ; fins large with small fulcra anteriorly and lepidotrichia distally bifurcated. Dorsal and anal fins triangular and of much the same size, dorsal fin opposed to the space between pelvic and anal fins ; pectoral fin with rays jointed to their base, and pelvics short based ; anal fin triangular, without fringe, similar in shape to pelvics, caudal fin deeply cleft and inequilateral. Skull with well-developed rostrum, oblique suspensorium and medium-sized orbit ; opercular larger than subopercular, with antero-dorsal dermohyal, but no ventral accessory bone in opercular series ; suborbitals present, and row of supraorbitals between dermosphenotic and nasal bones. Branchiostegal rays numerous, teeth acutely conical and arranged in two series—inner row of well spaced, large laniaries and outer row of numerous, closely arranged teeth. Scales rhomboidal, often denticulated posteriorly, large ridge scales in front of median fins. Skull bones ornamented with tuberculations and striae of enamel.

TYPE SPECIES. *Elonichthys germari* Giebel.

REMARKS. It has been found necessary at the outset to redefine the genus *Elonichthys* Giebel in order that the genera dealt with in this paper may be more clearly separated from it, since most of them have at some time or another been included in the genus *Elonichthys*.

Family **COSMOPTYCHIIDAE** nov.

DIAGNOSIS. Body fusiform, dorsal fin arising well in front of anal fin, both fins triangular. Caudal fin deeply cleft, heterocercal and inequilateral. Pectoral fin with bases of principal rays unjointed, and pelvics long based. All fins with numerous small fulcra anteriorly and lepidotrichia distally bifurcated. Skull rounded anteriorly and without well-developed rostrum. Suspensorium oblique and orbit large. Antorbital bears teeth. Opercular much larger than subopercular with antero-dorsal dermohyal and antero-ventral accessory opercular. Branchiostegal rays numerous and suborbital series present. Scales rhomboidal with pronounced striae. Dentition consisting of a series of large laniaries flanked on outside by series of more numerous, smaller teeth.

REMARKS. I have erected this family to include the two Lower Carboniferous genera, *Watsonichthys* Aldinger and *Cosmoptychius* Traquair. These two genera show many resemblances, of which the single accessory opercular and the long based pelvics are probably the most significant.



This family is closely allied to Aldinger's (1937 : 376) group A of the family Acrolepididae and in fact is probably ancestral to this group. For example, the scale structure of *Watsonichthys* is very much that of the Acrolepid-type (Aldinger, 1937 : 257) and both *Plegmolepis* Aldinger and *Acropholis* Aldinger have accessory operculars.

### Genus *WATSONICHTHYS* Aldinger, 1937

1877a *Elonichthys* Traquair, *partim*, p. 430.

DIAGNOSIS (emended). Body fusiform ; dorsal fin arising well in front of anal, both fins triangular, but anal much extended and fringe-like in hinder half ; caudal fin deeply cleft and inequilobate ; pectoral fin with principal rays unjointed in proximal third of their length, pelvics long based ; all fins with numerous small fulcra anteriorly and lepidotrichia distally bifurcated. Skull without well-developed rostrum and with two pairs of extrascapulars, suspensorium oblique and orbit medium-sized with a sclerotic ring ; opercular much larger than subopercular with antero-dorsal dermohyal and antero-ventral accessory opercular, branchiostegal rays numerous, suborbitals present ; cranial roof bones and cheek bones ornamented with tubercles and ridges of enamel ; teeth consisting of well-formed, conical lanianaries and numerous smaller teeth ; scales rhomboidal with pronounced striae.

TYPE SPECIES. *Elonichthys pectinatus* Traquair.

REMARKS. When Aldinger erected this genus to incorporate *Watsonichthys pectinatus* (Traquair) he also tentatively included in it *Watsonichthys* (?) *aitkeni* (Traquair). However, as I shall show later in this paper, *Watsonichthys* (?) *aitkeni* does not in fact belong to the genus *Watsonichthys*.

There is one other species, *Watsonichthys lotzi* (Gürich) from the Upper Dwyka Shales of Ganikobis, South Africa, which appears to be a member of this genus (Gardiner, 1962).

### *Watsonichthys pectinatus* (Traquair) (Text-fig. 1)

- 1877a *Elonichthys* (?) *pectinatus* Traquair, p. 430.
- 1879 *Elonichthys pectinatus* Traquair : Traquair, p. 121.
- 1882 *Elonichthys pectinatus* Traquair : Traquair, p. 545.
- 1887 *Elonichthys pectinatus* Traquair : Traquair, p. 315.
- 1891 *Elonichthys pectinatus* Traquair : Woodward, p. 500.
- 1897 *Elonichthys pectinatus* Traquair : Traquair, p. 144 (name only).
- 1901 *Elonichthys pectinatus* Traquair : Traquair, pp. 82-87, text-fig. 1, pls. 13, 14, figs. 1-3.
- 1921 *Elonichthys pectinatus* Traquair : Stensiö, p. 219.
- 1925 *Elonichthys pectinatus* Traquair : Watson, pp. 851-853, text-fig. 21.
- 1937 *Watsonichthys pectinatus* (Traquair) Aldinger, pp. 207, 254-257, text-fig. 72.
- 1938 *Elonichthys pectinatus* Traquair : Moy-Thomas & Dyne, p. 462.
- 1954 *Elonichthys pectinatus* Traquair : Waterston, p. 64.

DIAGNOSIS (emended). A large species reaching almost one metre in length. Body fusiform and anal fin with distinct fringe posteriorly. See also Traquair, 1901 : 82.



HOLOTYPE. Scales, R.S.M. 1874.22.2, and counterpart from the Gilmerton Ironstone, Gilmerton, near Edinburgh, Lower Carboniferous Limestone Series.

MATERIAL. Specimens including the holotype from the Royal Scottish Museum and from the British Museum (Nat. Hist.). Approximately thirty specimens were examined, twelve of which showed well preserved skulls.

REMARKS. This species was included in the genus *Elonichthys* Giebel by both Traquair and Woodward, but Aldinger (1937 : 254) placed it in a new genus, *Watsonichthys*, because of the several differences he believed it showed from the genus *Elonichthys*. These differences are quite apparent, especially the pectoral fin with its unjointed lepidotrichia and the fringe to the anal fin, not to mention the opercular apparatus. The question of the opercular apparatus is not so clear, Traquair (1890 : 397) considers the presence of a ventral accessory bone ("Y") in front of the opercular to be quite a common feature of the genus *Elonichthys*. However, the type species *Elonichthys germari* Giebel, as far as I can judge, does not possess this accessory bone, neither do *Elonichthys serratus* Traquair or *Elonichthys pulcherrimus* Traquair (Moy-Thomas & Dyne, 1938, text-figs. 22-25). The species of *Elonichthys* which allegedly possess this accessory bone, *Elonichthys pectinatus* Traquair and *Elonichthys striatus* (Agassiz), are undoubtedly members of other genera and as such can be removed, *E. pectinatus* Traquair being placed in the genus *Watsonichthys* Aldinger (1937), and *E. striatus* (Agassiz) in the genus *Cosmoptychius* Traquair (1877) See p. 266. Thus if we amend the definition of the genus *Elonichthys* Giebel given by Aldinger (1937 : 16) to include the two following facts, first that the anal fin is triangular and without a fringe and second, that there is no ventral accessory bone in the opercular series (See p. 263), then it is quite clear that Aldinger was perfectly justified in erecting the genus *Watsonichthys* to include *Watsonichthys pectinatus* (Traquair).

DESCRIPTION. *The skull*. The general shape of the skull can be seen from Text-fig. 1. The snout is rounded and not produced into a rostrum as in the genus *Elonichthys* Giebel. The external bones of the skull are all strongly ornamented with tubercles and ridges of enamel. The extrascapulars, parietals and frontals are ornamented with tubercles which tend to become confluent, forming short ridges, and which follow the length of the bone. The ridges of enamel on the dermopterotics are somewhat longer. The infraorbitals and suborbitals are mainly covered by tubercles and a few short striae. The maxilla has tuberculations along its ventral margin, but the expanded part is ornamented by ridges and lines of tubercles running parallel with the dorsal and posterior margins. On the preopercular the tubercles follow the posterior margin. The opercular, subopercular, accessory opercular and dermohyal are all uniformly ornamented with tubercles and short striae which run concentrically round the bones. The tubercles on these opercular bones are often pointed and are invariably striated with delicate grooves which converge towards the apex of the tubercle and in this respect are similar to those found on the dermopterotics. The ornamentation of the lower jaw consists of short stout ridges of enamel which are sinuous, occasionally branched and which



more or less follow the length of the jaw. Interspersed among the ridges are more pointed tubercles. The ridges are characterized by delicate striae, similar to those described on the tubercles, which run from the grooves up to the crest of the ridge on both sides, giving a herring-bone appearance to the ridge when viewed from above. The branchiostegal rays are more delicately ornamented with ridges and tubercles, the tubercles often being striated.

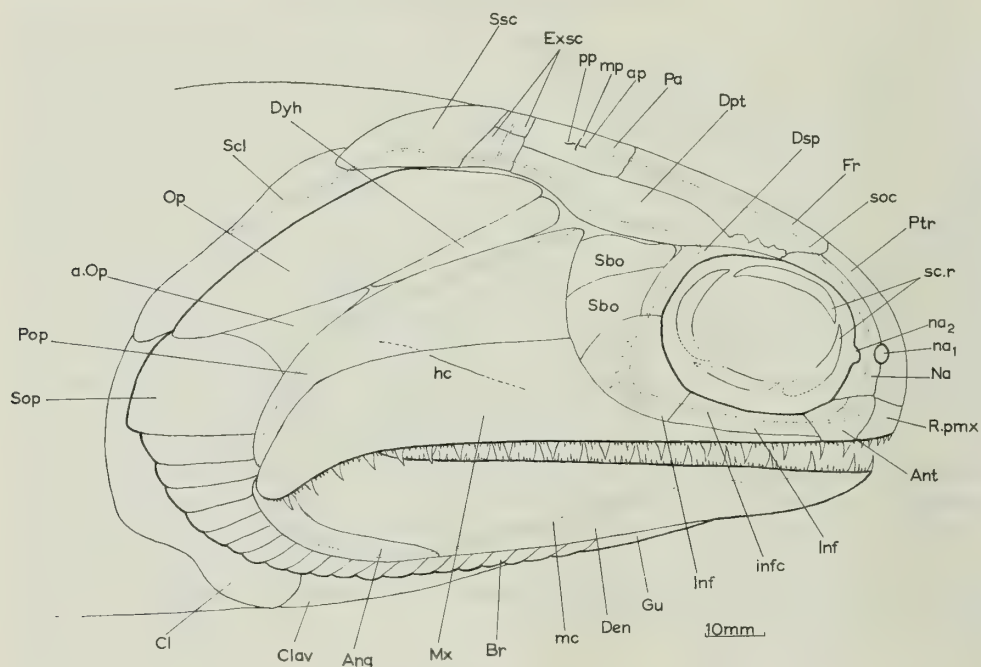


FIG. 1. *Watsonichthys pectinatus* (Traquair). Restoration of skull in lateral view.

The skull of *Watsonichthys* is long, with an oblique suspensorium and the orbit situated well forward. The large suprascapulars are joined to two pairs of extrascapulars anteriorly. The median pair of extrascapulars is small and square, while the members of the outer pair are larger and more rectangular. The parietals are quite large in this species and all three pit lines are clearly visible on them. The frontals are somewhat expanded anteriorly and the antero-lateral edge which joins the anterior margin of the dermopterotic has a characteristic wavy suture (R.S.M. 1896.34.1, 1896.34.2). Anteriorly the frontals meet the median postrostral and the nasals. The dermopterotic is a very long ossification which anteriorly just comes into contact with the most posterior edge of the nasal and extends the lateral edge of the skull roof quite considerably. The nasals and postrostral curve downwards to give the snout a rounded shape which can be clearly seen in a relatively uncrushed specimen preserved in the round (B.M.N.H., P.11576). Ventrally the postrostral joins the rostro-premaxillary and this latter bone forms the anterior



extremity of the upper jaw and bears four or five pointed teeth. The rostromaxillary can be seen on B.M.N.H., P.11577 where it has been displaced and lies in front of the skull. The antorbital bears a few teeth ventrally and the contained infraorbital sensory canal has the primitive "Y" shaped bifurcation. There are two members of the infraorbital series, a long ventral member which borders the lower margin of the orbit and a second considerably expanded bone which joins it posteriorly and forms part of the posterior rim of the orbit. This second infraorbital is much more plate-like, fitting neatly beneath the suborbitals. The sensory canal, as it passes through this infraorbital, gives off numerous finer branches posteriorly. Dorsally this infraorbital joins the dermosphenotic anteriorly and the second suborbital posteriorly. The dermosphenotic is a narrow but stout bone which dorsally fits under the lateral edge of the dermopterotic and extends anteriorly just to meet the nasal. Behind the dermosphenotic lies a pair of suborbitals. The orbit itself has an ossified sclerotic ring made up of four segments. The upper segment can be seen on R.S.M. 1896.34.1, where the centre is feebly ornamented with a few tubercles but the remainder is mainly smooth bone.

The maxilla is of the normal palaeoniscoid pattern and bears two series of teeth as in *Elonichthys* Giebel, a row of large pointed teeth interspersed with a series of much smaller teeth. The tooth series extends right up to the posterior extremity of the maxilla. The preopercular is a little higher than the maxilla, and the preopercular sensory canal passing along its length is distinctly elbowed about a third of the way up.

The opercular is approximately rhomboidal in outline with its antero-ventral margin cut away for the reception of the accessory opercular.

A conspicuous feature of the lateral wall of the skull is the presence of both "X" and "Y" bones, the upper of which is common in long-jawed palaeoniscoids. The terminology used in the past for these two bones is very confusing, but for the sake of completeness I will cite it. First the dorsal bone which lies in front of the opercular, between it and the dorsal edge of the preopercular. Traquair (1901 : 84) in describing *Watsonichthys pectinatus* (Traquair) referred to this bone as "X", but Watson (1925 : 819) in his description of *Cheirolepis trailli* Agassiz referred to the corresponding bone as "Y". Aldinger (1937 : 16) however called it a dorsal anteroperculum, but in recent times it has been given the name of dermohyal (Nielsen, 1936 : 42). Since there is in all probability a relationship between this dorsal bone and the underlying hyomandibular, I think the term dermohyal a convenient one and as such shall retain it.

Secondly, the ventral bone which lies between the antero-ventral corner of the opercular and the preopercular. Traquair (1877c : 47) first called this bone the suboperculum, then later referred to it as the interoperculum (1890 : 397). Later again Traquair (1901 : 62) considered it an "accessory plate", but in the same work (1901 : 84) in describing *Watsonichthys pectinatus* (Traquair) he calls it bone "Y". Watson (1925 : 819) in describing *Cheirolepis trailli* Agassiz referred to it as bone "X", while Aldinger (1937 : 16) considered it to be a ventral anteroperculum. Nielsen (1936 : 42) used the term ventral dermohyal for this bone, but Rayner



(1951 : 57) although doubting its relationship with the hyomandibular retains the term for the sake of convenience. Pehrson (1940) from a study of the development of the dermal bones of the skull of *Amia calva* believes that both the "X" and "Y" bones (of Watson, 1925 : 819) in *Cheirolepis trailli* came from primordia developed in relation to the preopercular canal. Stensiö (1947 : 149, 152) believes that both the dermohyal and bone "X" of Watson (1925 : 819) are anamestic components of the preopercular plate, corresponding to similar anamestic components of the preopercular plate in the Porolepiformes. Lehman (1947 : 17) follows Pehrson (1940) and Stensiö (1947) and has coined the term epipreopercular for the bone "X" of Watson (1925 : 819). Rayner (1951 : 57) however thinks that "the ventral dermohyal is simply an extra bone in the opercular series", and after studying other palaeoniscoids in which this bone occurs, *Watsonichthys*, *Cosmoptychius*, *Kentuckia* and *Rhabdolepis* I consider this to be the most sensible view and use the term accessory opercular when describing this bone.

The accessory opercular is triangular in outline with the ventral margin concave where it fits over the subopercular. Consequently the shape of the subopercular is altered for the reception of the accessory opercular, its dorsal margin not being straight as is the more normal condition, but convex. Between the opercular and the preopercular and above the accessory opercular lies the dermohyal. This bone is broadest dorsally and narrows almost to a point ventrally. From the angle of these opercular bones the suspensorium can be seen to be oblique. The subopercular is succeeded by approximately twenty branchiostegal rays and there is a median gular between the jaw rami.

*The Lower Jaw.* The greatest portion of the jaw is made up of the dentary. The surangular is relatively large and forms a neat socket for the articulating surface of the upper jaw. The remainder of the posterior edge is made up of the angular which is very stout near the jaw articulation. The upper margin of the jaw is straight, except posteriorly, where it extends upwards to give a high prominence to the back end of the jaw which bears the articulatory facet. The teeth are of two main sizes, the large ones which are smooth and with a well-defined enamel cap covering the last few mm. of tooth and which bear striations immediately below the cap, and the smaller tooth series which fills in the spaces between the larger teeth.

The palate has been adequately described by Watson (1925 : 851) and is very similar to that seen in *Namaichthys schroederi* Gürich (Gardiner, 1962).

Fragments of the hyobranchial apparatus can be seen in R.S.M. 1890.133.17, where several of the ceratobranchials of the left side are visible. These are long, smooth, and similar in size. The hyomandibular is stout and inclined, lying beneath the dermohyal and the posterior edge of the preopercular, and is similar in shape to that seen in *Pteronisculus* (Nielsen, 1942).

*The paired fins and their girdles.* The supracleithrum is large and extends down beyond the ventral limit of the opercular. The cleithrum is stout, distinctly curved and expanded ventrally and with large clavicles succeeding it anteriorly. The bones of the pectoral girdle are more or less longitudinally striated.



The pectoral fin has about fifteen to twenty rays, the first eight of which are the largest and are unjointed for the initial third of their length. The rays are delicately ornamented with a few oblique striae (R.S.M. 1890.104.11).

The pelvic fin is slightly smaller, with about twenty rays all jointed to their bases. The fin has a long base line, much longer than in *Elonichthys* Giebel, and in this respect it resembles both *Cheirolepis* Agassiz and *Cosmoptychius* Traquair. Both pectoral and pelvic fins bear numerous fulcra.

*The unpaired fins.* Both the dorsal and anal fins are large with stout rays. The dorsal fin has about thirty-five to forty rays which are strongly ornamented with longitudinal striae. There are four to six large ridge scales in front of the dorsal fin and the fulcral scales form a stout anterior border to the fin.

The anal fin has about thirty five rays and a distinct fringe posteriorly ; in this respect it resembles *Pygopterus* Agassiz. The ornamentation is slighter than on the dorsal fin and there is only one large ridge scale preceding it. The fulcral scales are again large and on some specimens the radials supporting the fin can be made out. The radials are long, the first radial articulating with about six lepidotrichia, its distal end being much widened. The remaining radials are only slightly thickened distally (R.S.M. 1892.138.5, B.M.N.H., P.11577).

The caudal fin is heterocercal, inequilateral and deeply cleft.

*The squamation.* The characteristic ornamentation and shape of the scales of this species have been well described and figured by Traquair. The scales are ornamented with ridges of enamel which run longitudinally along the length of the scale and terminate in nine or more serrations or teeth posteriorly and to which the specific name *W. pectinatus* (Traquair) refers. The ridges often branch once anteriorly and once posteriorly. The ridge scales of the axial lobe are ornamented on their free areas with small striated tubercles.

### Genus *COSMOPTYCHIUS* Traquair, 1877b

1835 *Amblypterus* Agassiz, *partim*, 2, 1, p. 111, pl. 4b, figs. 3-6.

1857 *Rhabdolepis* Troschel, *partim*, p. 16.

1890 *Elonichthys* Traquair, *partim*, pp. 390, 396.

**DIAGNOSIS** (emended). Body deeply fusiform ; dorsal fin arising well in front of anal, both fins large and triangular, the former being slightly larger ; caudal fin powerful, deeply cleft and inequilateral ; pectoral fin with rays articulated except just at commencement of first two rays at lateral margin of fin, and pelvics long based ; all fins with numerous small fulcra anteriorly and lepidotrichia distally bifurcated. Skull rounded anteriorly, without a well developed rostrum and with only one pair of extrascapulars, suspensorium very oblique and orbit large ; opercular long and narrow, much longer than subopercular with antero-dorsal dermohyal and antero-ventral accessory opercular. Preopercular very narrow and produced antero-dorsally to fit over the top of first suborbital, branchiostegal rays numerous, suborbitals present. Head bones sculptured with sharply defined, nearly parallel, branching and anastomosing ridges of enamel ; gape wide, teeth consisting



of closely set, rather small, conical lanianaries with outer series of much smaller teeth ; scales large, rhomboidal, with pronounced, oblique striae, flank scales higher than broad.

TYPE SPECIES. *Amblypterus striatus* Agassiz.

REMARKS. This genus was erected by Traquair (1877b : 553 ; 1877c : 43) to incorporate the single species described by Agassiz (1835 : 111) as *Amblypterus striatus*. Traquair (1890 : 390), however, decided that this species did not in fact belong to a new genus, as he had previously supposed, neither did it belong to the essentially Permian genus *Amblypterus* Agassiz (1835 : 111), but that it belonged to the genus *Elonichthys* Giebel, a view supported later by Woodward (1891 : 491), who lists *Cosmoptychius* Traquair as being synonymous with *Elonichthys*. Watson (1928 : 49), when describing the neurocranium of *striatus* Agassiz, refers the species to the genus *Cosmoptychius* Traquair. Finally, Aldinger (1937 : 312) pointed out that from the shape of the parasphenoid alone *striatus* Agassiz differed so much from the genus *Elonichthys* that it was necessary to retain the genus *Cosmoptychius* Traquair for its reception. He then linked *Cosmoptychius* with *Nematoptychius* Traquair and *Pygopterus* Agassiz in the new family Pygopteridae.

### *Cosmoptychius striatus* (Agassiz)

(Text-figs. 2, 3)

- 1835 *Amblypterus striatus* Agassiz, 2, 1, p. 111, pl. 4b, figs. 3-6.
- 1837 *Amblypterus striatus* Agassiz : Paterson, p. 153.
- 1854 *Amblypterus striatus* Agassiz : Morris, p. 317.
- 1857 *Rhabdolepis striatus* (Agassiz) Troschel, p. 16.
- 1877b *Cosmoptychius striatus* (Agassiz) Traquair, p. 553.
- 1877c *Cosmoptychius striatus* (Agassiz) : Traquair, p. 43, pl. 2, fig. 7, pl. 3, figs. 1-8.
- 1888 *Cosmoptychius striatus* (Agassiz) : Sauvage, p. 42, pl. 16, fig. 3.
- 1890 *Elonichthys striatus* (Agassiz) Traquair, pp. 390, 396.
- 1891 *Elonichthys striatus* (Agassiz) : Woodward, p. 491.
- 1901 *Elonichthys* (*Cosmoptychius*) *striatus* (Agassiz) : Traquair, p. 84, footnote 1.
- 1907 *Elonichthys striatus* (Agassiz) : Traquair, p. 107.
- 1928 *Cosmoptychius striatus* (Agassiz) : Watson, p. 49, text-figs. 1-3.
- 1937 *Cosmoptychius striatus* (Agassiz) : Aldinger, p. 312.
- 1954 *Elonichthys striatus* (Agassiz) : Waterston, p. 67.

DIAGNOSIS (emended). Fishes not exceeding 28 cm. in total length, body fusiform, length of head contained four times and greatest depth of body three times in total body length. Dorsal and anal fins similar in size, pelvic fin long based. Lepidotrichia of fins striated partly longitudinally and partly diagonally ; ornamentation of scales characteristic ; four ridge scales in front of dorsal, one in front of caudal fins, ridge scales of axial lobe commencing some way behind dorsal fin. See also Traquair 1877c : 43.

SYNTYPES. R.S.M. 1878.18.1, 1878.18.2 and 1878.18.3, all from the Calciferos Sandstone Series, Wardie, Edinburgh. I designate R.S.M. 1878.18.2 as the lectotype.



**MATERIAL.** Specimens including the syntypes from the Royal Scottish Museum and from the British Museum (Nat. Hist.). Fifteen specimens were examined, in five of which the skull was well preserved and in counterpart.

**DESCRIPTION.** *The skull.* The dermal bones of the skull and the sensory canal system, as far as can be determined, are shown in Text-fig. 2. The snout is rounded as in *Watsonichthys pectinatus* (Traquair) and not produced into a rostrum as in the genus *Elonichthys* Giebel.

The skull roofing bones are all ornamented with ridges of enamel which run parallel to one another and which occasionally branch and anastomose : nowhere do these ridges give way to tubercles. On the frontals, nasals and rostral these ridges follow the length of the bone, but on the dermopterotic the ridges follow a more sinuous course, starting at the posterior, inferior corner, they pass upwards, then curve gently downwards and then more gently upwards again, to reach the anterior edge of the bone, only occasionally branching and anastomosing. The ridges on the extrascapulars and suprascapulars run transversely from the mid-line of the skull out to the lateral edges. The ornamentation of the opercular series, maxilla, suborbitals, branchiostegal rays and lower jaw has already been figured by Traquair (1877c, pl. 3, fig. 3). On the opercular the ridges on the posterior half of the bone follow the outline of that bone, while on the anterior half they run up and across more or less diagonally. The ridges of ornament on the subopercular and branchiostegal rays run antero-posteriorly dividing and anastomosing. On the supracleithrum these ridges run diagonally across the length of the bone. However, on the maxilla the ridges of enamel follow the contour of the bone, passing upwards from the postero-ventral corner, across the top of the bone and then curving downwards when they reach the anterior edge ; several ridges run lengthways along the ventral edge. The majority of the ridges of enamel on the maxilla run parallel to one another along the whole of their length, as though engraved there by a precision tool. Over the anterior two-thirds of the preopercular the ridges pass from the mid-line of the bone, upwards to the dorsal edge, and downwards and backwards in a diagonal fashion to the ventral edge, giving the bone a herring-bone type of patterning. On the dermohyal the striae follow its long axis, whilst on the accessory opercular they run more obliquely. Of the suborbital series, the ornament on the dorsal member runs across horizontally while that of the ventral member runs across from the anterior edge, curves downwards and then follows the ventral edge of the bone. On the dermosphenotic the ridges in part follow the length of the bone (dorsally) and in part run horizontally across it (ventrally). Again on the second infraorbital the ridges run across almost horizontally. Ventrally on the lower jaw the ridges of ornament follow its entire length, but from the mid-line they run diagonally forwards and upwards to the dorsal jaw edge. In summing up this ornamentation I quote Traquair (1877c : 44) : " Nothing can exceed the beauty of the sculpture of the external surfaces of these facial bones, which consist of delicate yet sharply defined, nearly parallel, and slightly wavy, branching and anastomosing ridges ".



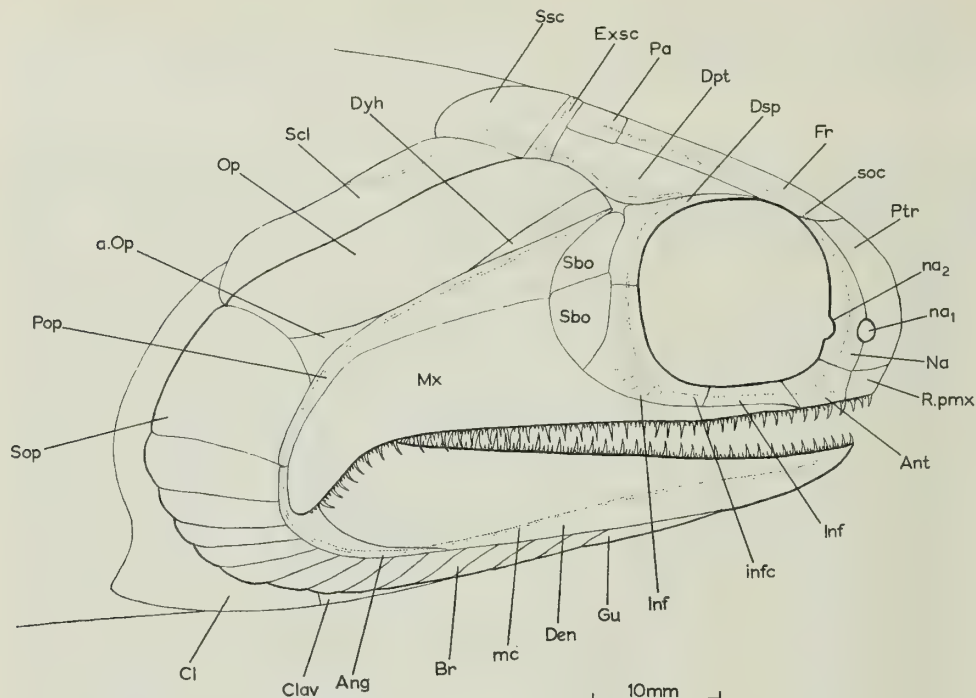


FIG. 2. *Cosmoptychius striatus* (Agassiz). Reconstruction of skull in lateral view.

The skull is characterized by its oblique suspensorium and the make up of the opercular apparatus. The suprascapulars are stout, bluntly rounded posteriorly and joined to a single pair of narrow extrascapulars. The parietals are small and square and the greater portion of the skull roof is made up by the large rectangular frontals. The dermopterotics are small and do not extend far enough to meet the nasals anteriorly. The postrostral is a stout ossification whilst the nasals are thinner and more delicate. Ventrally the nasals join the toothed antorbital and there is some evidence of a rostromaxillary bone in front of the antorbital and beneath the postrostral. The snout is bluntly rounded (R.S.M. 1859.33.71 and counterpart). There are but two members of the infraorbital series. The first is short and rectangular joining the antorbital anteriorly and the maxilla ventrally. The second infraorbital has an expanded basal portion which is concave posteriorly where it fits under the suborbital series. Dorsally the second infraorbital meets the dermosphenotic. The dermosphenotic forms the upper posterior margin to the orbit and extends forwardly just to meet the frontal. The suborbital series consists of two bones, the lower of which is the larger; both are approximately triangular in outline (R.S.M. 1859.33.71). Occasionally these two bones are fused into a single ossification (R.S.M. 1875.29.153). The maxilla is of the normal palaeoniscoid pattern and curves slightly upwards before it meets the antorbital. The ventral



margin bears teeth along its entire length, the teeth being in two series ; a series of stout, sharp, incurved, conical teeth which are closely set, and an outer series of much smaller teeth. The preopercular is a very narrow bone, as narrow as that seen in the genus *Cycloptychius* Young. Anteriorly it is produced almost to a point where it fits over the upper of the two suborbitals. Dorsally the preopercular does not extend far enough to meet the dermopterotic. Above the preopercular is a wedge-shaped dermohyal tapering to a point ventrally. Dorsally it abuts on to the dermopterotic. The opercular is also a narrow bone, with both the antero-dorsal and antero-ventral corners bevelled to admit the dermohyal and the accessory opercular respectively. Similarly the antero-dorsal corner of the subopercular is bevelled to make room for the accessory opercular. Apart from this, however, the subopercular is nearly square, but rather broader posteriorly. The branchiostegal rays number approximately fifteen, with a lozenge-shaped gular plate anteriorly.

*The lower jaw.* The mandible is stout with an upper margin which curves slightly upwards at its extremity. The greater portion of the outer surface of the jaw is made up by the dentary. The angular, which is a stout ossification, makes up the posterior border. The posterior end of Meckel's cartilage is completely ossified, forming a stout articular. The upper border of the dentary supports a series of large, curved teeth, which posteriorly are directed forwards. These laniary teeth are closely set, the distance between them being less than their own length, and by comparison with *Watsonichthys pectinatus* (Traquair) they are relatively small teeth. Outside these laniary teeth is a series of much smaller teeth, less than half the size of the inner series. The shelf on which these laniary teeth are set is overlapped at its inner edge by the coronoid bone.

*Palate.* The palatoquadrate cartilage is completely ossified and the most extensive bone is the entopterygoid (pterygoid of Watson, 1925). The entopterygoid is distinctly concave and of pronounced semi-cylindrical shape. Posteriorly it joins the smaller ectopterygoid. The ectopterygoid bears a series of pointed teeth continuous with those on the palatine, the palatine being attached to the anterior end of the ectopterygoid. Posteriorly the ectopterygoid is fused to the stout quadrate. Above the ectopterygoid is an expanded, more lightly ossified metapterygoid, and the suprapterygoid series forms an anterior extension to the metapterygoid and also the hinder margin to the deep notch through which the maxillary and mandibular branches of the fifth nerve passed. The general make up of the palatoquadrate apparatus then is not very different from that described for *Nematoptychius greenocki* (Traquair) by Watson (1928, text-fig. 7).

The hyomandibular, the only other visible component of the visceral arch skeleton, is much more distinctly elbowed than in *Pteronisculus* White. It can be clearly seen in specimen R.S.M. 1926.57.22, and is blade-shaped dorsally with a stout axial ridge. Ventrally the bone is elbowed and the lower shaft is circular in cross section. The hyomandibular lies immediately beneath the preopercular and is similar in shape.

*The Neurocranium.* This has been adequately described by Watson (1928 : 49, text-figs. 1-4).



*The paired fins and their girdles.* The primary girdle is ossified, both the scapulocoracoid and mesocoracoid regions being apparent. Specimen R.S.M. 1857.33.71 shows clearly four radial elements (Text-fig. 3). The second radial from the lateral edge of the fin is hour-glass shaped, whilst the two innermost members are stout and almost straight rods. Distally the first two radials (numbering from the lateral edge) articulate with four smaller ossifications; these probably represent the ossified distal cartilages of the radials. The third radial articulates directly with six lepidotrichia and the fourth probably with three lepidotrichia. The lepidotrichia number about nineteen, and they are jointed throughout their length except at the bases of the first two rays of the lateral margin. The lepidotrichia are delicately ornamented with two distinct ridges anteriorly, which run along the length of the ray, and posteriorly with short diagonal ridges of enamel that run from about the mid-line out and away from the fin base, to the posterior edge of the ray.

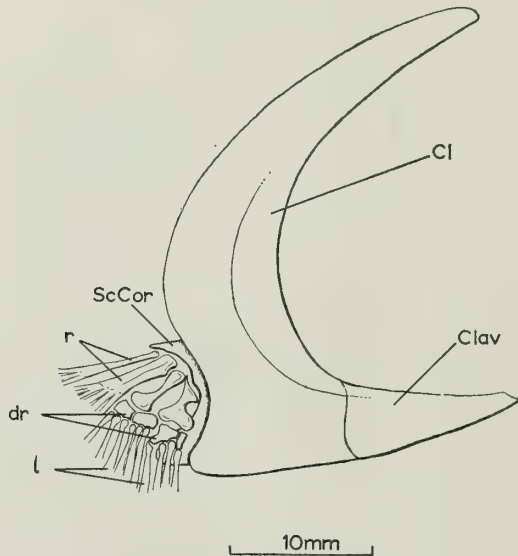


FIG. 3. *Cosmoptychius striatus* (Agassiz). Reconstruction of pectoral girdle. Mainly from R.S.M. 1857.33.71.

The pelvic fin is very long based with about forty to forty-five fin rays, and similar ornamentation to the pectorals, except that instead of two ridges of enamel running lengthways along the rays anteriorly there is only one. Both pectoral and pelvic fins bear fulcral scales.

*The unpaired fins.* Both dorsal and anal fins are triangular, the dorsal being somewhat the larger. Both have about forty lepidotrichia and are fringed anteriorly by pointed fulcral scales. The ornamentation of these two fins is essentially similar to that on the pectoral as far as the anterior fin rays are concerned, but on the more



posterior rays there is only one longitudinal ridge (Traquair, 1877, pl. 13, fig. 3). The caudal fin is heterocercal, deeply cleft and inequilobate.

*The squamation.* The scales from the middle of the flank are nearly twice as deep as broad. The scale ornamentation consists of fine, sharply defined, parallel ridges of enamel which pass diagonally downwards and backwards across the scale. These ridges sometimes branch, and occasionally anastomose. The ridges extend beyond the posterior scale margin to give it a delicately serrated appearance (i.e. the margin is delicately denticulated). Woodward's (1891 : 491) statement that none of the scales is posteriorly serrated is thus erroneous.

### Family ACROLEPIDAE

DIAGNOSIS. See Aldinger, 1937 : 32, 250.

REMARKS. The genus *Mesonichthys* gen. nov. clearly belongs to Group A of the family Acrolepidae (Aldinger, 1937 : 250) and bears many resemblances to *Acrolepis sedgwicki* Agassiz, in particular the abnormally high position of the external nares (see Westoll in Aldinger, 1937, text-fig. 74).

### Genus *MESONICHTHYS* nov.

1886 *Elonichthys* Traquair, *partim*, p. 440.

1937 *Watsonichthys* Aldinger, *partim*, p. 256.

DIAGNOSIS. Body fusiform ; dorsal fin arising well in front of anal, both fins triangular, acuminate and similar in size ; caudal fin deeply cleft and inequilobate ; pectoral fin long, with principal rays unjointed in proximal third of their length, pelvics short based ; all fins have numerous fulcra anteriorly and lepidotrichia distally bifurcated. Snout rounded anteriorly and not produced into a rostrum. Jaw suspension only moderately oblique and opercular more than twice as high as subopercular. Orbit large with well developed sclerotic ring ; dermohyal present but no accessory opercular ; suborbitals present ; angle of preopercular approximately 60° ; cranial roof bones and cheek bones ornamented with ridges of enamel ; teeth of two sizes, larger conical lanianaries being closely set with smaller tooth series interspersed ; scales rhomboidal with pronounced ridges.

TYPE SPECIES. *Elonichthys aitkeni* Traquair.

REMARKS. *Mesonichthys aitkeni* (Traquair) was placed in the genus *Elonichthys* Giebel by Traquair (1886 : 440). Aldinger (1937 : 256) concluded that this species was not a member of the genus *Elonichthys* because the principal lepidotrichia of the pectoral fins were unjointed and suggested its inclusion in the genus *Watsonichthys*. He also pointed out (p. 207) that the form of the opercular, the scale ornamentation and the shape of the metapterygoid suggested it was an acrolepid. However, the genus *Watsonichthys* is characterized by, amongst many other features, the presence of an accessory opercular. No accessory opercular occurs in *Mesonichthys aitkeni* (Traquair), and it is necessary to erect a new genus for the reception of this species.



***Mesonichthys aitkeni*** (Traquair)  
(Text-fig. 4)

- 1874 *Acrolepis* sp. Aitken, p. 36.  
 1886 *Elonichthys aitkeni* Traquair, p. 440.  
 1890 *Elonichthys aitkeni* Traquair : Ward, p. 174, pl. 6, figs. 9, 12.  
 1891 *Elonichthys aitkeni* Traquair : Woodward, p. 490.  
 1895 *Elonichthys aitkeni* Traquair : Bolton, pl. 3, fig. 14.  
 1898 *Elonichthys aitkeni* Traquair : Welburn, p. 426, pl. 62, fig. 5.  
 1901 *Elonichthys aitkeni* Traquair : Traquair, pp. 77-80, pls. 16, 17, figs. 1-7.  
 1907 *Elonichthys aitkeni* Traquair : Rogers, p. 394.  
 1919 *Elonichthys aitkeni* Traquair : Pruvost, p. 404, pl. 28, fig. 11.  
 1925 *Elonichthys aitkeni* Traquair : Watson, p. 855, text-fig. 23, p. 862, text-fig. 29.  
 1930 *Elonichthys aitkeni* Traquair : Pruvost, p. 124.  
 1932 *Elonichthys aitkeni* Traquair : Susta, p. 136, pl. 1, figs. 16, 17.  
 1934 *Elonichthys aitkeni* Traquair : Keller, p. 50, pl. 5, fig. 10.  
 1937 *Elonichthys aitkeni* Traquair : Aldinger, p. 207.  
 1937 *Watsonichthys* (?) *aitkeni* (Traquair) Aldinger, p. 256.  
 1939 *Elonichthys aitkeni* Traquair : White, p. 42.  
 1941 *Elonichthys aitkeni* Traquair : Demanet, p. 174, pl. 11, figs. 3-10.  
 1943 *Elonichthys aitkeni* Traquair : Heide, p. 29, fig. 2.  
 1945 *Elonichthys aitkeni* Traquair : Dorsman, p. 78, pl. 11, fig. 3.  
 1955 *Elonichthys aitkeni* Traquair : Heide, p. 74, pl. 17, fig. 32.

DIAGNOSIS (emended). Fishes not exceeding 18 cm. in total length, body fusiform, length of head contained five times and greatest depth of body four times in total body length. Lepidotrichia slender and smooth. Scales of moderate size, deeper than broad on the flank and ornamented with prominent striae which run obliquely across the scale. Striae straight, rarely bifurcated or interpolated, and run parallel to one another. See also Traquair, 1901 : 77.

LECTOTYPE. From Traquair's original description (1886 : 440) of the species only one specimen is identifiable. This specimen was figured in a later paper by Traquair (1901, pl. 16, fig. 1) and was an imperfect fish from the collection of J. Aitken. It came from the "Copy" Coal Mine, Cliviger, Lancashire. Woodward (1891 : 490) nominated this same specimen as the type. Unfortunately, even when figured by Traquair in 1901, this specimen had already been lost. Since it seems very unlikely that this lectotype of Woodward's will ever be found, I nominate as the neotype B.M.N.H., P.6100 from the Culm-Measures, Instow, North Devon, figured by Traquair (1901, pl. 17, fig. 7).

MATERIAL. Specimens, including the neotype, from the British Museum (Nat. Hist.) and the Geological Survey Museum. Ten specimens were examined.

REMARKS. One specimen in the Geological Survey Museum, No. 4520 and counterpart, figured by Traquair (1901, pl. 16, fig. 2) was probably one of the specimens on which he based his original description (1886 : 440).

DESCRIPTION. *The skull.* The shape of the skull is given in Text-fig. 4. The snout is rounded as in *Watsonichthys pectinatus* (Traquair). The external skull bones are all very strongly ornamented with ridges of enamel. On the frontals,



parietals, dermopterotics and suprascapulars these ridges of enamel follow the length of the bone. Many of the ridges run the whole length of these bones and a small percentage of them occasionally branch, but not usually more than once. On the postrostral the ridges of enamel are shorter and break up into tubercles anteriorly, while on the nasals the ridges are longer and follow the long axis of the bone. The ridges of enamel on the dermosphenotic and the two suborbital bones, however, run across the bones from front to back, a few of the ridges branching, more particularly on the suborbitals. Again, on the more posterior infraorbital the ridges run horizontally on its dorsal region, but ventrally the ridges become more vertical in their course. The ornamentation on the antorbital and rostro-premaxillary consists of shorter ridges running parallel to the long axis of the fish. Along the ventral edge of the maxilla the ridges of enamel are also short and follow the bone margin. On the greater portion of the maxilla the ridges are long and pass upwards and forwards to the dorsal margin, occasionally branching. On the dorsal extremity of the preopercular the ridges run across the bone from front to back, but more ventrally the ridges branch, become much more sinuous and sweep slightly upwards. The ornamentation on the dermohyal consists of well marked ridges which run more or less parallel to the short axis of this bone. On the opercular some of the ridges are very long and pass diagonally from the posterior ventral corner to the dorsal anterior corner, and the rest of the ridges run more or less parallel to these. The ridges which ornament the preopercular make a far different pattern from that seen on any of the other skull bones. The ridges sweep upwards from the posterior ventral corner towards the dorsal margin, curve downwards until they almost reach the middle point of the anterior margin and then curve back on themselves and follow a sinuous course back to the ventral edge. The effect of this is to give a roughly oval-shaped central area to the preopercular. The ornamentation of the mandible is somewhat variable but basically the ridges of enamel follow the length of the bone ventrally, while for the major portion of the mandible the ridges sweep upwards and forwards to the dorsal margin of the jaw. On the branchiostegal rays and gular plate the ridges follow the long axis of the bones and branch occasionally, usually not more than once. The pectoral girdle is well ornamented and on the cleithrum, supracleithrum and clavicles the ridges tend to follow the contours of the bones and occasionally bifurcate. The sclerotic ring is also ornamented but only with very feeble striae.

The skull of *Mesonichthys* is compact as in *Acrolepis* and not drawn out anteriorly as in *Elonichthys*. The orbit is situated well forward and the suspensorium is only moderately oblique. The suprascapulars are not as large as those in *Watsonichthys* and are joined to a single pair of narrow extrascapulars. The small, square parietals are preceded by a large pair of rectangular frontals. The dermopterotic is almost triangular in outline and extends laterally beyond the upper margin of the dermohyal nearly to meet the dorsal-most suborbital. Anteriorly the dermopterotic tapers to a point where it meets the nasal. The frontals join the postrostral and the nasals anteriorly. The postrostral is a large ossification, V-shaped where it fits between the two frontals (B.M.N.H., P.600). The nasal tapers sharply dorsally, joins the



antero-lateral edge of the frontal for a short distance and fits neatly over the anterior extremities of the dermopterotic and the dermosphenotic. Both the postrostral and the nasals curve downwards anteriorly, to give the snout a rounded shape (B.M.N.H., P.6100). Ventrally the postrostral joins the rostro-premaxillary. Both the rostro-premaxillary and the antorbital, which meets the rostro-premaxillary posteriorly, bear pointed teeth (B.M.N.H., P.36246).

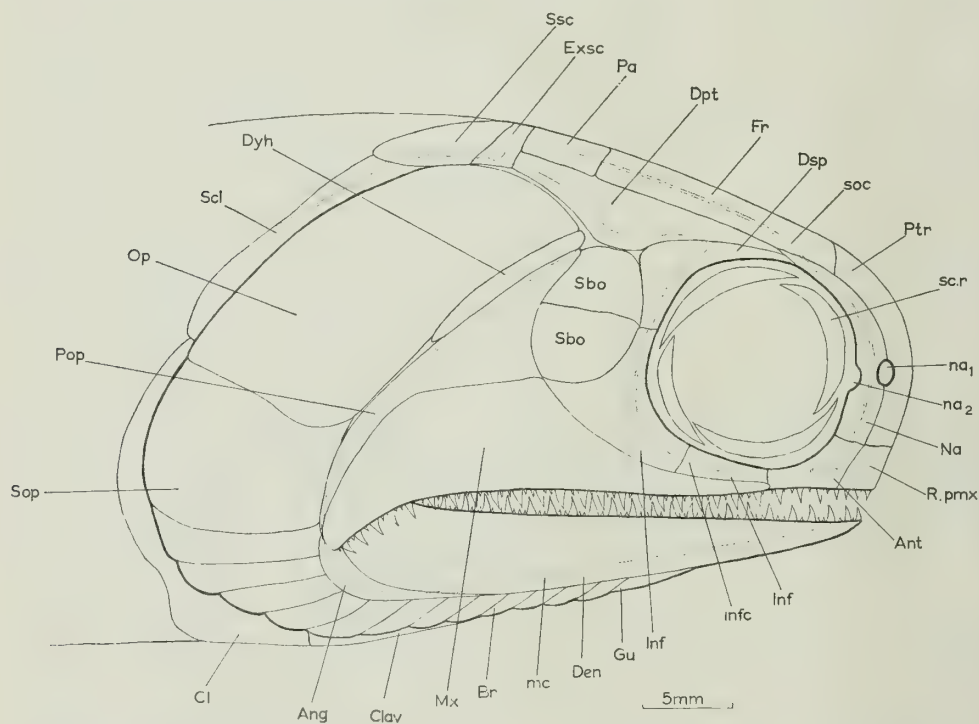


FIG. 4. *Mesonichthys aitheni* (Traquair). Reconstruction of the dermal bones of the skull in lateral view.

There are only two members of the infraorbital series. The first is a short rectangular bone which joins the antorbital anteriorly and the maxilla ventrally. Posteriorly it is united with the second infraorbital. The second infraorbital forms half of the posterior margin of the orbit and is concave anteriorly. This infraorbital is also concave posteriorly where it fits under the second suborbital bone, whilst ventrally its margin is convex. Dorsally the second infraorbital joins the dermosphenotic. The dermosphenotic forms the upper posterior quarter of the orbit's margin, and posteriorly it is concave where it fits round the first suborbital.

The suborbital series consists of two bones of approximately the same size and which together are oval in outline. The lower suborbital is rounded ventrally while the upper is rounded dorsally, the suture between them is straight.



The orbit has a sclerotic ring made up of four segments of which the two dorsal members are the largest.

The maxilla is of normal palaeoniscoid shape except that the anterior ventral margin turns slightly upwards before it meets the antorbital. The ventral margin bears teeth along the whole of its length. The teeth are of two sizes, a series of large conical teeth interspersed with a series of smaller teeth. The preopercular is a high bone with its posterior margin much nearer the vertical than that of *Elonichthys* or *Watsonichthys*. Anteriorly the margin of the preopercular is distinctly concave for the reception of the two suborbitals. Dorsally the preopercular does not meet the dermopterotic. Behind the preopercular lies a narrow dermohyal. The dermohyal tapers ventrally almost to a point, but dorsally it is rounded and extends a short distance beyond the dorsal limit of the preopercular.

The opercular is rectangular in outline with its dorsal margin gently rounded. The opercular is more than twice as high as the subopercular and more nearly vertical than the opercular in *Watsonichthys*. The preopercular is succeeded by twelve to fifteen branchiostegal rays and there is a median angular between the jaw rami.

*The lower jaw.* The greater portion of the lower jaw consists of dentary with the angular bone making up the posterior margin. The angular, when viewed from the outer jaw surface, does not extend very far along the ventral margin. The upper margin of the jaw is straight and bears teeth of two sizes. There is a series of large conical teeth, set much closer together than in the genus *Elonichthys* and a smaller tooth series which fills in the spaces between these larger teeth.

*The Palate.* The palate, hyobranchial apparatus and part of the neurocranium have been adequately described by Watson (1925 : 855, 862, figs. 23, 29).

*The Paired fins and their girdles.* The supracleithrum does not extend beyond the ventral limit of the opercular. The cleithrum is a stout ossification and is succeeded by an equally stout clavicle.

The pectoral fin is composed of between twenty and twenty-two rays, the principal members of which are unjointed for the initial third of their length. The rays are smooth and the anterior edge of the fin bears a row of fulcral scales. These fulcral scales form a pronounced fringe.

The pelvic fin is smaller with about fifteen rays, all jointed to their bases. The fin is relatively small, short based, and unornamented. Anteriorly there are numerous small fulcra.

*The Unpaired fins.* Both dorsal and anal fins are triangular, similar in size and with thirty-eight to forty-two rays. The fulcral scales are long and the fin rays are smooth, apart from a single longitudinal furrow just before they bifurcate. The caudal fin is heterocercal, inequilobate and deeply cleft.

*The squamation.* The scales have been adequately described and figured by Traquair. One peculiar ornamental character noted by Traquair is that the lowermost ridge on most of the body scales is united to the ridge above it, resulting in a broad, ventral ridge.

There is one large ridge scale in front of the anal fin, and several preceding the dorsal fin. The ridge scales of the axial lobe arise some distance behind the dorsal fin.



Family **PYGOPTERIDAE**

DIAGNOSIS. See Aldinger, 1937 : 309.

Genus **NEMATOPTYCHIUS** Traquair, 1875

1844 *Pygopterus* Agassiz, 2, 2, p. 78 (undefined).

1867 *Pygopterus* Traquair, *partim*, p. 701, pl. 45.

DIAGNOSIS (emended). Body elongate : dorsal fin situated far back nearly opposite anal, both triangular and of moderate size : caudal fin heterocercal and deeply cleft : paired fins moderate in size, pectoral fin with principal rays unarticulated for a short distance from origin, remainder of fin with closely articulated rays : all fins with distinct but small fulcra anteriorly and lepidotrichia distally bifurcated. Skull with distinct rostrum, very oblique suspensorium and relatively small orbit with stout sclerotic ring. Opercular long and narrow dorsally and no antero-dorsal dermohyal or antero-ventral accessory opercular. Rostro-premaxillary present and also suborbital series, branchiostegal rays numerous : head bones ornamented with ridges and tubercles, gape wide, dentition consisting of inner series of large, stout, conical laniaries, few in number, and outer series of more numerous smaller teeth ; scales small, only slightly imbricating, those of the flank much higher than broad with relatively large peg-and-socket articulation. Scale ornament consisting of delicate ridges of enamel.

TYPE SPECIES. *Nematoptychius greenocki* (Traquair).

REMARKS. This genus was erected by Traquair (1875 : 258) to incorporate the single species previously described by him (1866 : 597) as *Pygopterus greenockii*. The same author (1876 : 262) described a second species, *Nematoptychius gracilis*, but decided later (1890 : 391) that this was synonymous with *Nematoptychius greenocki* (Traquair). One of the specimens (R.S.M. 1875.29.127) which Peach (1872 : 109) used to erect the species *Pygopterus elegans* (nomen nudum) is also synonymous with *Nematoptychius greenocki* (Traquair).

***Nematoptychius greenocki*** (Traquair)

(Text-figs. 5-8)

1844 *Pygopterus greenockii* Agassiz, 2, 2, p. 78 (undefined).

1866 *Pygopterus greenockii* Traquair, p. 597.

1867 *Pygopterus greenockii* Traquair : Traquair, p. 701, pl. 45, figs. 1-4.

1872 *Pygopterus elegans* Peach, p. 109 (nomen nudum).

1875 *Nematoptychius greenockii* (Traquair) Traquair, p. 258, pl. 16, figs. 7-11.

1876 *Nematoptychius gracilis* Traquair, p. 262.

1877b *Nematoptychius greenockii* (Traquair) : Traquair, p. 577.

1877c *Nematoptychius greenockii* (Traquair) : Traquair, pp. 14, 15, pl. 1, figs. 7-11.

1879 *Nematoptychius greenockii* (Traquair) : Traquair, pp. 118, 128.

1890 *Nematoptychius greenockii* (Traquair) : Traquair, pp. 391, 398.

1891 *Nematoptychius greenocki* (Traquair) : Woodward, p. 458.

1907 *Nematoptychius greenocki* (Traquair) : Traquair, p. 111.

1909 *Nematoptychius greenocki* (Traquair) : Traquair, p. 116, pl. 26.

1925 *Nematoptychius greenocki* (Traquair) : Watson, p. 858, text-fig. 26.

1928 *Nematoptychius greenocki* (Traquair) : Watson, pp. 55, 59, text-figs. 7, 11.



1954 *Nematoptychius greenocki* (Traquair) : Waterston, p. 59.

1954 *Nematoptychius gracilis* Traquair : Waterston, p. 61.

DIAGNOSIS (emended). Fishes not exceeding 48 cm. in total length, body elongated, length of head contained almost five times and greatest depth of body more than five times in total body length. Dorsal and anal fins similar in size and opposed to one another, pelvic fin moderately long based. Lepidotrichia of fins closely articulated and not noticeably ornamented ; ornamentation of scales characteristic. See also Traquair, 1909 : 117.

SYNTYPES. R.S.M. 1926.57.44 and 1950.38.87, from the Calciferos Sandstone Series, Wardie, Edinburgh. Lectotype, R.S.M. 1926.57.44 as designated by Waterston (1954 : 59) and by Woodward (1891 : 458).

MATERIAL. Specimens, including one of the syntypes from the Royal Scottish Museum and from the British Museum (Nat. Hist.). Twenty-four specimens were studied including three showing the skull roofing bones and a fourth in which the head was uncrushed and preserved in the round.

REMARKS. *Nematoptychius greenocki* is widely distributed throughout the Lower Carboniferous rocks of eastern Scotland occurring from the Wardie Shales right up into the Upper Limestone Series. Traquair (1909 : 120) commenting on the predacious habits of some of the larger palaeoniscoids notes that in the abdominal cavity of one specimen of *N. greenocki* are the remains of a good-sized *Acanthodes*.

DESCRIPTION. *The skull.* The bones of the skull and course of the sensory canals are shown in Text-fig. 5. The most distinctive features are the pronounced rostrum and the absence of both dermohyal and accessory opercular bones.

The skull roofing bones are all ornamented with ridges of enamel, which in places give way to tubercles. On the parietals, frontals, dermopterotics and postrostral bones the ridges of enamel run more or less longitudinally along the length of these bones, the ridges are relatively short, dividing and anastomosing, and in places giving way to tubercles. The ridges of enamel on the extrascapular run across the bones, so that they are more or less continuous with those on the parietals and dermopterotics, whilst the suprascapular has very few ridges and is mainly tuberculated. The rostro-premaxillary also has an ornamentation of tubercles, but the nasals and the sclerotic ring are smooth. The maxilla has two distinct ornamentations, the oral margin is covered by large tubercles of enamel, while the remainder of the bone is covered by ridges, which sweep up and round the bone, running parallel with its posterior and superior borders. The infraorbitals and antorbitals are again tuberculated and the dermosphenotic has both tubercles and short ridges of enamel. On the suborbitals ridges of enamel run more or less dorso-ventrally. On the preopercular the ornamentation consists of short striae, and on the opercular the ridges follow the outline of that bone, running from top to bottom. The subopercular has fewer ridges, but more tubercles while the branchiostegal rays have mainly ridges which divide and anastomose and run more or less diagonally across the bones. The mandible is covered by short ridges and tubercles along its entire length ; the tubercles are more numerous anteriorly.



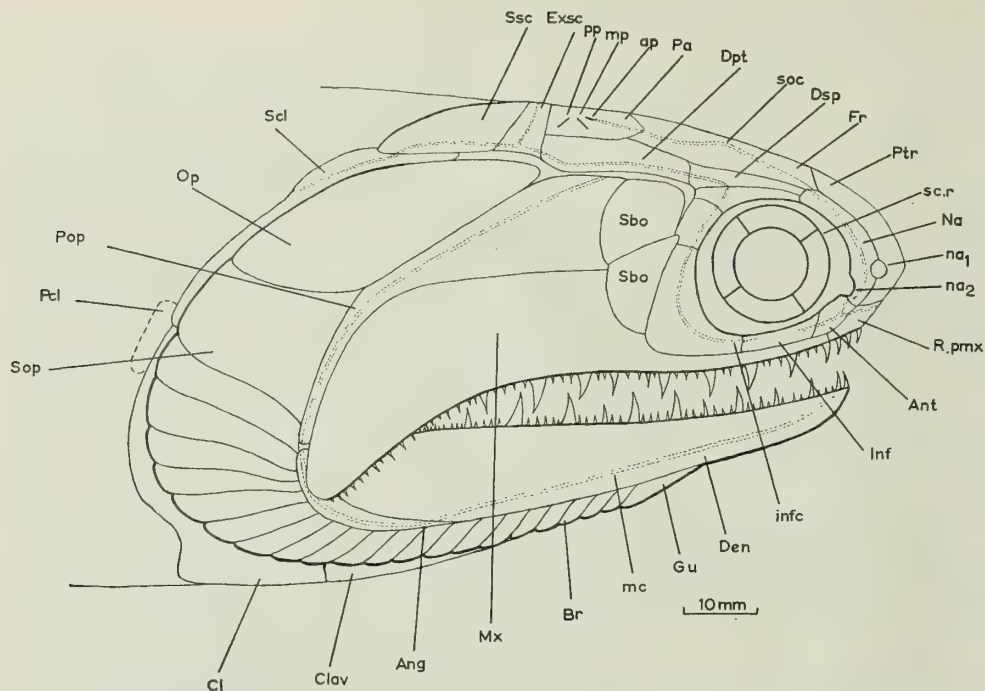


FIG. 5. *Nematoptychius greenocki* (Traquair). Reconstruction of skull in lateral view.

The skull of *N. greenocki* is long with an oblique suspensorium and the orbit situated well forward. The suprascapulars just meet in the mid-line anteriorly as do the single pair of extrascapular bones which precede them. The remainder of the skull roofing bones are known with much more certainty in this species than in most other palaeoniscoids of comparable age, since there are several specimens in which the cranial buckler has been preserved uncrushed, and some in which the whole head has been preserved in the round (R.S.M. 1892.137.6, 1891.111.9, 1950.38.87).

The paired parietals are rectangular with their anterior margins produced into a point (Text-fig. 6) and the sutures between them and the frontals anteriorly and the dermopterotics laterally are strongly digitated. The frontals are long and all the sutures between them and the other skull roofing bones equally toothed and digitate. Laterally the frontal is bordered by the dermopterotic, dermosphenotic and the nasal, whilst anteriorly the postrostral has a V-shaped insertion between the two frontals.

The lateral wall of the skull roof is comprised of three bones, the dermopterotic, the dermosphenotic and the infraorbital-supraorbital. The dermopterotic is the largest of these three bones and anteriorly joins the dermosphenotic. The dermo-



sphenotic passes forward to meet the nasal. The infraorbito-supraorbital lies alongside the dermosphenotic and overlaps it to a slight degree. Anteriorly the infraorbito-supraorbital also joins the nasal. The postrostral is only slightly curved from side to side in its posterior half, giving but a slight convexity to the dorsal surface ; however, the anterior half of the bone is strongly curved in a transverse as well as a longitudinal direction, giving the head the typical palaeonisciform profile, that is a distinct rostrum. The radiation centre of the bone lies in its most arched part, in other words that region which forms the anterior tip of the rostrum.

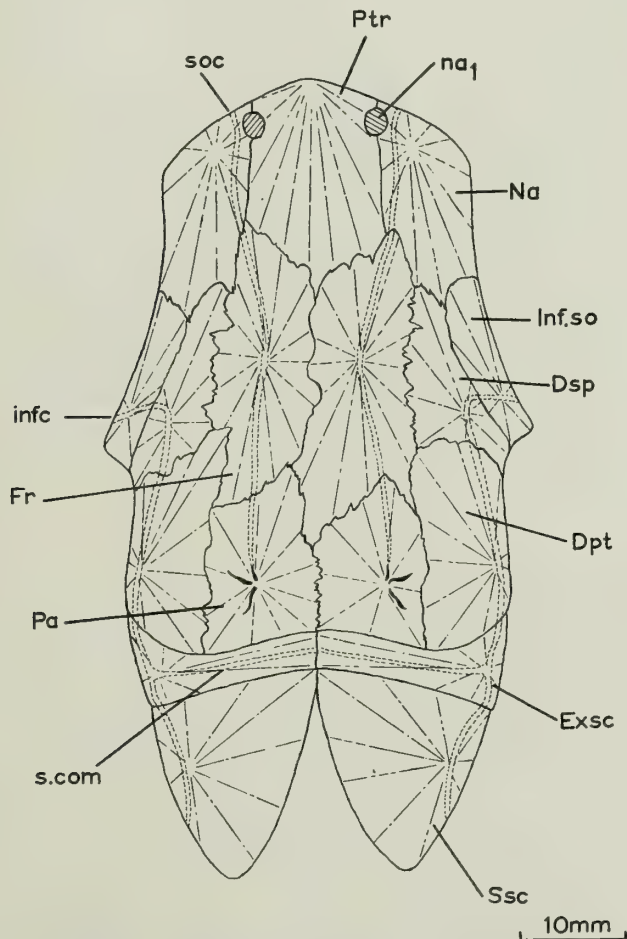


FIG. 6. *Nematoptychius greenocki* (Traquair). Dorsal view of skull roofing bones. From R.S.M. 1892.157.6, 1891.111.9 and 1890.78.4.

The nasal is stout and broad and its lateral margin forms together with the dorsal margin of the antorbital a distinct emargination ( $na_2$ ) which indicates the position



of the posterior nostril. The anterior nostril ( $na_1$ ) lies between the nasal and the postrostral. Posteriorly the nasal joins the frontal, dermosphenotic and the infraorbito-supraorbital. Anteriorly the postrostral meets the paired, toothed rostro-premaxillaries. The rostro-premaxillary can be distinguished on several specimens (B.M.N.H., P.11569, R.S.M. 1889.5.1) but its relationship to the neighbouring bones can best be seen on specimen R.S.M. 1950.38.87 from which Text-fig. 7 has been reconstructed. Most of the snout region in this specimen consists of an internal cast of the bones, and this shows the articulations of the individual bones more clearly. The rostro-premaxillaries overlap the anterior end of the postrostral, and running across the back of the rostro-premaxillaries in a transverse direction is a distinct groove (eth. com.). This groove in the rostro-premaxillaries carried the ethmoidal commissure. That this deduction as to the course of the ethmoidal commissure is correct and that Nielsen's (1942 : 136, fig. 32) view that the ethmoidal commissure ran along the back of the postrostral in *Pteronisculus gunnari* (Nielsen) is wrong is borne out by the course of the infraorbital sensory canal through the antorbital. The antorbital has the characteristic fork of the infraorbital canal in it, and also bears a rostral process through which the infraorbital canal passes (Text-fig. 7). This process fits behind the rostro-premaxillary, and is so positioned that the contained infraorbital canal is continuous with the groove (ethc.) in the back of the rostro-premaxillaries. The groove in the back of the postrostral in *Rhadinichthys fusiformis* Traquair has been correctly interpreted by Moy-Thomas & Dyne (1938 : 455, text-fig. 17) to be for the articulation of the front end of the palate and not a sensory canal groove, whilst a similar groove in the postrostral of *Pteronisculus gunnari* (Nielsen) is for the same purpose and not for the path of the ethmoidal commissure as it was interpreted by Nielsen (1942 : 136). The ethmoidal commissure, as far as can be judged, is never associated with the postrostral (see discussion).

The antorbital articulates with the nasal and rostro-premaxillary anteriorly and with the maxilla ventrally. Posteriorly the antorbital joins the first member of the infraorbital series. There are three infraorbitals of which the second is by far the largest (Text-fig. 5). The third infraorbital is short and dorsally joins the lateral corner of the infraorbito-supraorbital. Behind the infraorbital series are two suborbitals. Both suborbitals are strongly convex posteriorly where they fit into the anterior edges of the preopercular and maxillary bones. The ventral suborbital is roughly triangular in outline. The maxilla is of the normal palaeoniscoid outline, but not very high and curving upwards quite markedly towards its anterior extremity. The ventral margin of the maxilla bears teeth along its entire length ; the teeth are in two series, a series of stout, large, conical, slightly incurved teeth with smooth enamel caps and an outer series of smaller teeth. The preopercular is again of the normal palaeoniscoid form, but the preopercular sensory canal ends on the dorsal margin behind the anterior extremity of the bone.

The suspensorium is oblique and the opercular is not very large in comparison to the skull size. There are no accessory bones and the subopercular is less than half as high as the opercular. The preceding branchiostegal rays number approxi-



mately twenty and there is a small median gular plate. The orbit contains a large, smooth sclerotic ring which is probably composed of four segments (R.S.M. 1890.78.4 and an unregistered specimen from Straiton Oil Works).

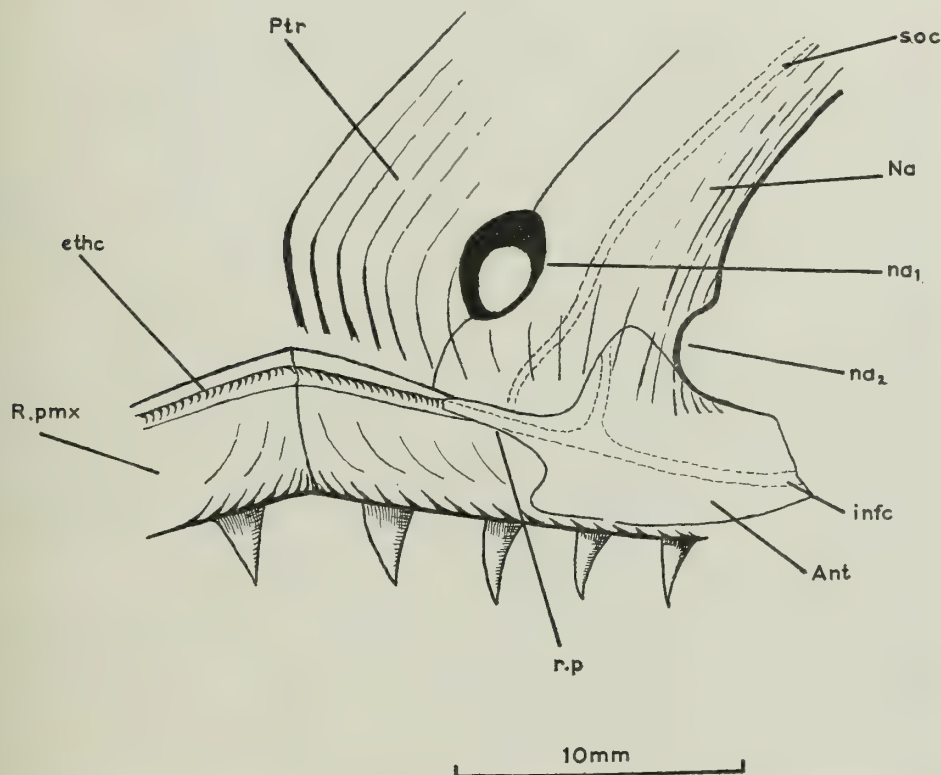


FIG. 7. *Nematoptychius greenocki* (Traquair). Snout region. From R.S.M. 1890.78.4.

*Lower jaw.* This has been adequately described by Watson (1925, text-fig. 11).

*Palate.* This has likewise been well described by Watson (1925, text-fig. 26 ; 1928, text-fig. 7).

*The paired fins and their girdles.* Of the pectoral girdle, the supracleithrum and cleithrum are ornamented with delicate tubercles and ridges of enamel. There is a pair of stout clavicles and posterior to the supracleithrum there appears to be a single member of the postcleithral series. There are ossified radials present, probably four in number ; these are hour-glass shaped and increase in length from the lateral towards the medial edge of the fin. The lepidotrichia of the pectoral fin number some fifteen members and the principal rays are unarticulated for a slight distance from their origin.

The pelvic fin has an extended base line and is composed of thirty or more rays.

*The unpaired fins.* The dorsal and anal fins are large and situated far back,



opposite one another, the anal being slightly the larger. The dorsal fin is formed of about forty rays and the anal forty-five. Both fins are triangular with closely articulated rays. The caudal fin is heterocercal, deeply cleft and inequilobate.

In several specimens some of the ossifications of the axial skeleton and the unpaired fins could be investigated in fair detail (R.S.M. 1950.38.87, 1889.5.1, etc.) (Text-fig. 8). The endoskeleton of the dorsal fin consists of several radials, each including two ossifications, viz. an axonost and a baseost. The axonost is long and circular in cross section and the anterior axonosts articulate direct with the basidorsals. The hindmost axonosts appear to be continuous with the basidorsals. The baseosts are small and rather hour-glass shaped. There are no distal ossifications beyond them as described by Nielsen (1942 : 243) in *Pteronisculus aldingeri* (Nielsen). Nothing more of the dorsal fin support could be made out and it was impossible to decide if there was a large plate in the axonost series as in *Pteronisculus aldingeri* (Nielsen).

The endoskeleton of the anal fin is far more satisfactorily preserved (R.S.M. 1950.38.87). It consists of a single series of radials numbering probably sixteen, which are longest in the anterior region and become successively shorter posteriorly (Text-fig. 8). These radials probably represent the fusion of two elements, the baseosts and axonosts, to give a single ossification. In *Pygopterus nielseni* Aldinger (1937, fig. 42) similarly only one series of ossifications is found in the endoskeleton of the anal fin. In *Pteronisculus* there are two ossifications and it seems likely that the distal series here must represent ossifications in the distal radial segments, a tentative suggestion already put forward by Nielsen (1942 : 249).

*The axial skeleton.* Anterior to the dorsal fin several basidorsals can be made out ; these consist of a small, four-sided proximal plate and a distal process. An independent supraneural, associated with the distal process, can be made out in one instance.

Above the radials of the anal fin occur a series of ossifications associated with the notochord. These ossifications consist of a basiventral which has become fused with the unpaired infrahaemals. These haemal arches become progressively longer posteriorly. From the distance apart of these haemal arches in the posterior region it seems probable that they alternated with small intraventrals as in *Pteronisculus aldingeri* (Nielsen).

The remaining ossifications in the caudal region are very similar to those described by Nielsen (1942 : 216) for *Pteronisculus aldingeri* (Nielsen), with the unpaired distal parts of the haemal arches being widened so as to form hypurals, which possibly include radial elements. Dorsally in the caudal region there is but a single series of basidorsal elements. Nothing further of the axial skeleton could be determined with any degree of certainty.

*Squamation.* The scales have been well described by Traquair (1909 : 118), and are peculiar in form. The scales in the flank regions are much higher than broad and the exposed area is more or less rhomboidal, but as Traquair points out "the acute angles are here the postero-superior and the antero-inferior". The scales are only very slightly imbricating and the ornamentation consists of delicate



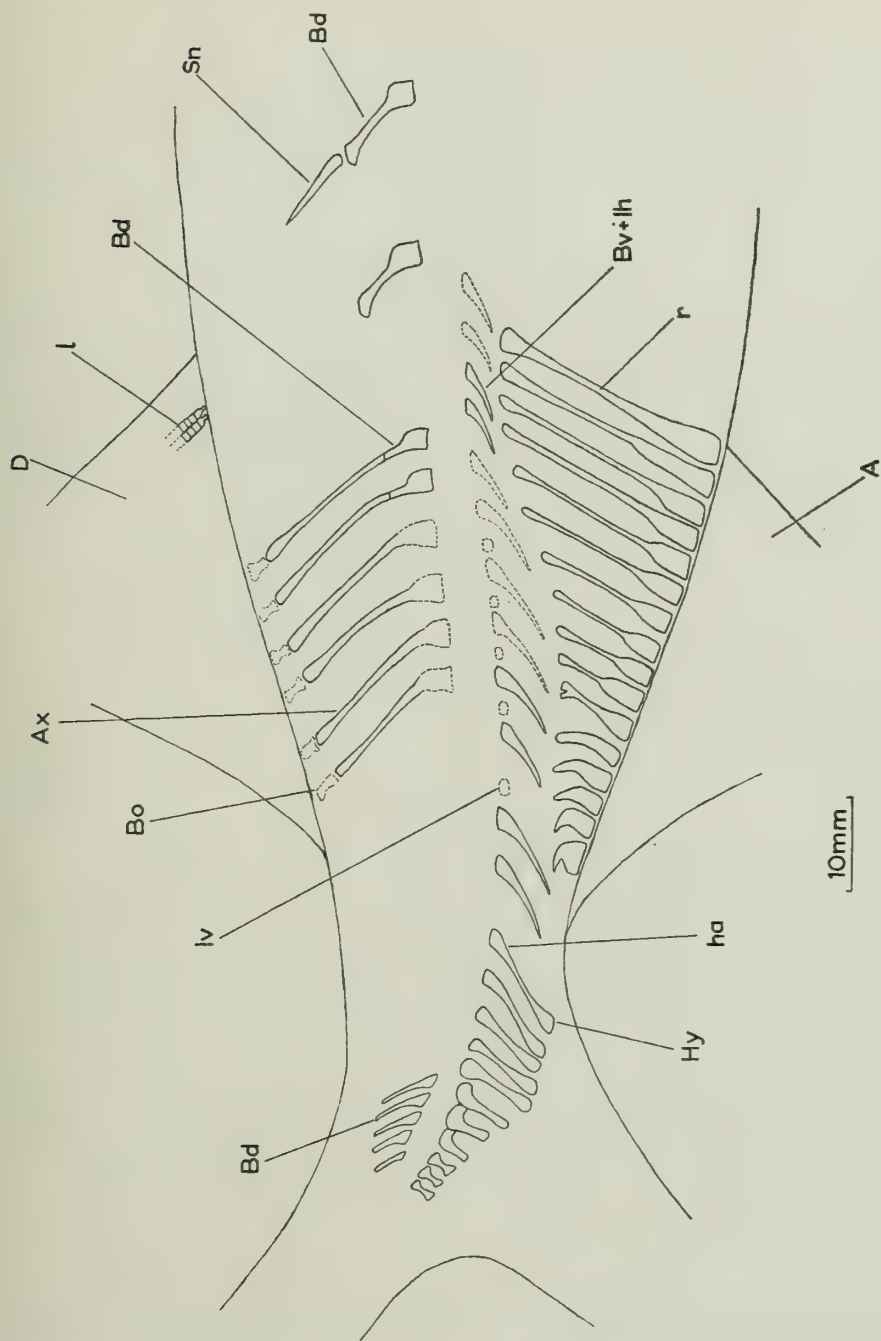


FIG. 8. *Nematopterychius greenochi* (Traquair). Axial skeleton. Mainly from R.S.M. 1890.78.4, 1889.5.1 and 1950.38.87.



wavy ridges, branching and anastomosing and directed obliquely downwards. The scales on the ventral part of the body are very small and equilateral in shape. On one specimen (B.M.N.H., P.11558) where that region showed at all clearly I have observed a small patch of smaller scales beneath the posterior end of the dorsal fin which is not continuous with the normal scale rows. In this *N. greenocki* shows something approaching the condition seen in *Pygopterus nielsenii* Aldinger (1937, fig. 37).

### Family RHABDOLEPIDAE nov.

DIAGNOSIS. As genus for the *Rhabdolepis*.

REMARKS. From my description of *Rhabdolepis* it is clear that this genus does not belong in the family Elonichthyidae, where both Aldinger (1937 : 376) and Romer (1945 : 579) placed it ; further it does not fit into any other previously described family. A new family, Rhabdolepidae, is therefore erected to include this single genus.

From the scale structure, body form and disposition of the fins, the family Rhabdolepidae seems fairly close to the family Elonichthyidae.

### Genus RHABDOLEPIS Troschel, 1857

- 1829 *Palaeoniscum* Bronn, *partim*, p. 483.
- 1833 *Amblypterus* Agassiz, *partim*, 2, 1, pp. 4, 37.
- 1873 *Leiolepis* Goldenberg, p. 5 (name only).
- 1891 *Elonichthys* Woodward, *partim*, p. 491.
- 1905 *Pygopterus* Langenhan, p. 10.

DIAGNOSIS (emended). Trunk deeply fusiform ; dorsal fin partly in advance of, partly opposing the anal, both large, acuminate and distinctly triangular, anal slightly larger than dorsal. Caudal fin powerful, deeply cleft and heterocercal. Paired fins large, pelvic pair smaller than pectorals, arising midway between the latter and the anal. All fins with minute fulcra anteriorly and with rays articulated and distally bifurcating. Skull with oblique suspensorium, prominent rostrum and delicate sclerotic ring. Opercular long and very narrow and with accessory opercular separating it completely from subopercular. Suborbital series present and branchiostegal rays numerous ; skull roofing bones ornamented with tubercles, other skull bones striated. Dentition consisting of inner series of large, stout, conical laniaries, few in number, and outer series of much smaller and far more numerous teeth ; scales small, as broad as deep on flank, ornamented with irregular, delicate, oblique striae, terminating as series of digitations on anterior overlapped border. On flank scales, three or four striae run nearly parallel with inferior scale border.

TYPE SPECIES. *Palaeoniscum macropterus* Bronn.

REMARKS. The type species was first assigned to the genus *Palaeoniscum* by Bronn (1829 : 483), but Agassiz (1833 : 3) realizing that it did not in fact belong to this genus, placed it in a new genus *Amblypterus*. He also (Agassiz, 1833 : 4)



listed several species to be included within the genus *Amblypterus*, but did not designate any one of them as the type species.

Troschel (1857 : 15) decided that *Amblypterus macropterus* Agassiz, *Amblypterus eupterygius* Agassiz, *Amblypterus striatus* Agassiz, *Amblypterus agassizii* Münster and *Amblypterus ornatus* Giebel on their dentition were very different from all the other species placed in the genus *Amblypterus* by Agassiz, so he removed them and founded the genus *Rhabdolepis* for their reception, but like Agassiz he omitted to designate any one of them as the type species of his new genus *Rhabdolepis*. However, Sauvage (1888 : 59) quite correctly designated *Amblypterus macropterus* Agassiz as the type species of the genus *Rhabdolepis* Troschel even though he incorrectly attributed the species to Agassiz instead of to Bronn.

Thus *Palaeoniscum macropteron* Bronn must be regarded as the type species of the genus *Rhabdolepis* Troschel.

My reason for dealing in this paper with an essentially Permian genus is that like *Watsonichthys* Aldinger and *Cosmoptychius* Traquair it possesses an accessory opercular bone. This accessory opercular bone, however, completely separates the opercular from the subopercular and this condition is very similar to that described by Casier (1952, text-fig. 1) in *Osorioichthys marginis* (Casier) from the Devonian. What Casier (1952, text-fig. 1) labelled subopercular in fact corresponds to the accessory opercular in *Rhabdolepis macropterus* (Bronn) (Text-fig. 9) and what he termed the first branchiostegal ray is undoubtedly the true subopercular, and thus his argument that this first branchiostegal in *Osorioichthys marginis* is equivalent to the interopercular in higher fishes is completely erroneous. [Note : Casier originally described this fish as *Stereolepis marginis* n. gen., n. sp.; however the genus was already preoccupied so he (1954) erected the new genus *Osorioichthys* for its reception.]

### *Rhabdolepis macropterus* (Bronn)

(Text-fig. 9)

- 1829 *Palaeoniscum macropteron* Bronn, pp. 483, 493.
- 1833 *Amblypterus macropterus* (Bronn) Agassiz, **2**, 1, pp. 4, 31, pl. 1, figs. 4-7, pl. 3, figs. 1-4.
- 1833 *Amblypterus eupterygius* Agassiz, **2**, 1, pp. 4, 36, pl. 1, fig. 8, pl. 3, figs. 5, 6.
- 1847 *Amblypterus macropterus* Agassiz : Goldfuss, p. 20, pl. 5, figs. 1-8.
- 1848 *Amblypterus macropterus* Agassiz : Giebel, p. 252.
- 1848 *Amblypterus eurypterygius* Agassiz : Giebel, p. 253.
- 1857 *Rhabdolepis macropterus* (Agassiz) Troschel, p. 15, pl. 2, fig. 15.
- 1857 *Rhabdolepis eupterygius* (Agassiz) Troschel, p. 15, pl. 2, fig. 14.
- 1873 *Amblypterus eupterygius* Agassiz : Goldenberg, 1, p. 5, pl. 1, fig. 2.
- 1877b *Rhabdolepis macropterus* (Bronn) : Traquair, p. 552.
- 1877c *Rhabdolepis macropterus* (Bronn) : Traquair, pl. 2, fig. 6.
- 1888 *Rhabdolepis macropterus* (Agassiz) : Sauvage, p. 59.
- 1891 *Elonichthys macropterus* (Bronn) Woodward, p. 491.
- 1892 *Amblypterus traquairi* Pohlig, p. 63, pl. 7, fig. 4.
- 1905 *Amblypterus* sp., Langenhan, pp. 9, 11, pl. 1c, fig. 17, pl. 1e, figs. 1, 4a, b.
- 1905 *Pygopterus antiquus* Langenhan, pp. 10, 11, pl. 1e, figs. 3a, b, pl. 1c, figs. 10-14, 16.
- 1905 *Amblypterus duvernoyi*? (Agassiz) : Langenhan, p. 10, pl. 1e, fig. 1.
- 1905 *Amblypterus traquairi* Pohlig : Langenhan, p. 10, pl. 1e, figs. 2a, b, pl. 3, fig. 4, pl. 4, figs. 2, 5, pl. 6, fig. 5.



- 1905 *Amblypterus elegans* Langenhan, p. 11, pl. 1e, figs. 5a, b, pl. 2, fig. 2.  
 1905 *Amblypterus gracilis* Langenhan, p. 11, pl. 2, fig. 1, pl. 4, fig. 6.  
 1905 *Amblypterus elongatus* Langenhan, p. 11, pl. 2, fig. 3, pl. 6, fig. 1.  
 1905 *Amblypterus regelii* Langenhan, p. 11, pl. 5, fig. 1.  
 1905 *Rhabdolepis macropterus* (Bronn) : Langenhan, p. 12, pl. 6, fig. 4.  
 1937 *Rhabdolepis macropterus* (Bronn) : Aldinger, p. 209.

DIAGNOSIS (emended). A species of moderate to large size, but not exceeding 40 cm. in total length. Length of head nearly equal to maximum depth of trunk and contained about four and a half times in total body length. Both dorsal and anal fins large, triangular and concavely cut out behind. Lepidotrichia of fins longitudinally striated. Opercular completely separated from subopercular by accessory opercular. Scales in anterior trunk region with delicately denticulated hinder margin, while ornamentation finishes in series of digitations on anterior overlapped border. Further back on trunk region hinder margins of scales without serrations. Probably three ridge-scales in front of dorsal fin, two in front of caudal fin and three very large ones in front of anal fin ; ridge-scales on axial lobe of tail commence just behind dorsal fin.

SYNTYPES. *Olim* H. G. Bronn Collection, from the Lower Permian of Saarbrück, Lebach and Boerschweiler, Germany. Searching the literature and contacting many German Museums has failed to reveal what was the subsequent fate of the Bronn Collection, thus I propose as the neotype B.M.N.H., P.3453 and counterpart P.2072, nearly complete fish from the Lower Permian, Lebach, Germany.

MATERIAL. Specimens from the British Museum (Natural History) and the Stuttgart Museum. Approximately twenty-five specimens were examined.

REMARKS. It was Troschel (1857 : 15) who first realized that *Amblypterus macropterus* (Bronn) did not agree in structure with the other species assigned to the genus *Amblypterus* by Agassiz (1833 : 4) and founded the new genus *Rhabdolepis* for its reception. Traquair (1877b : 552) followed Troschel in keeping *Amblypterus macropterus* (Bronn) in the genus *Rhabdolepis*. Woodward (1891 : 437, 491) also realised that this species did not belong to the same genus as *Amblypterus latus* Agassiz, but put *macropterus* Bronn in the genus *Elonichthys* Giebel. Aldinger (1937 : 209) correctly recognized that *macropterus* Bronn, on the nature of the opercular apparatus alone, did not belong to *Elonichthys*, and resurrected Troschel's genus *Rhabdolepis* for its reception.

From my description it is clear that *Palaeoniscum macropterus* Bronn was correctly placed in the genus *Rhabdolepis* by Troschel.<sup>1</sup>

DESCRIPTION. *The skull.* The shape and arrangement of the dermal bones of the skull are shown in Text-fig. 9. The most characteristic features are the accessory opercular completely separating the opercular from the subopercular, the delicate sclerotic ring and the presence of a rostrum.

The skull roofing bones are ornamented mainly with tubercles, but also with a

<sup>1</sup> Acanthodian remains are frequently found in the abdominal cavity of some of the larger specimens of this species.



few very short ridges of enamel. On the suprascapulars, extrascapulars, parietals, frontals, dermopterotics, dermosphenotics and nasals the tubercles run more or less from the ossification centres of these bones to their edges. The infraorbitals and antorbital bones are also tuberculated, but the remainder of the skull bones are delicately striated. On the maxilla the fine ridges of enamel run for a short distance upwards and forwards from the postero-ventral corner, but on the remainder of that bone the ridges follow the outline more closely. On the preopercular the ridges follow the length of the bone, whilst on the suborbitals, opercular, subopercular and accessory opercular they run more concentrically.

The ornamentation of the lower jaw consists of longer but finer ridges which run along the length of the bone dividing and anastomosing occasionally. On the branchiostegal rays and median gular the ridges are very delicate.

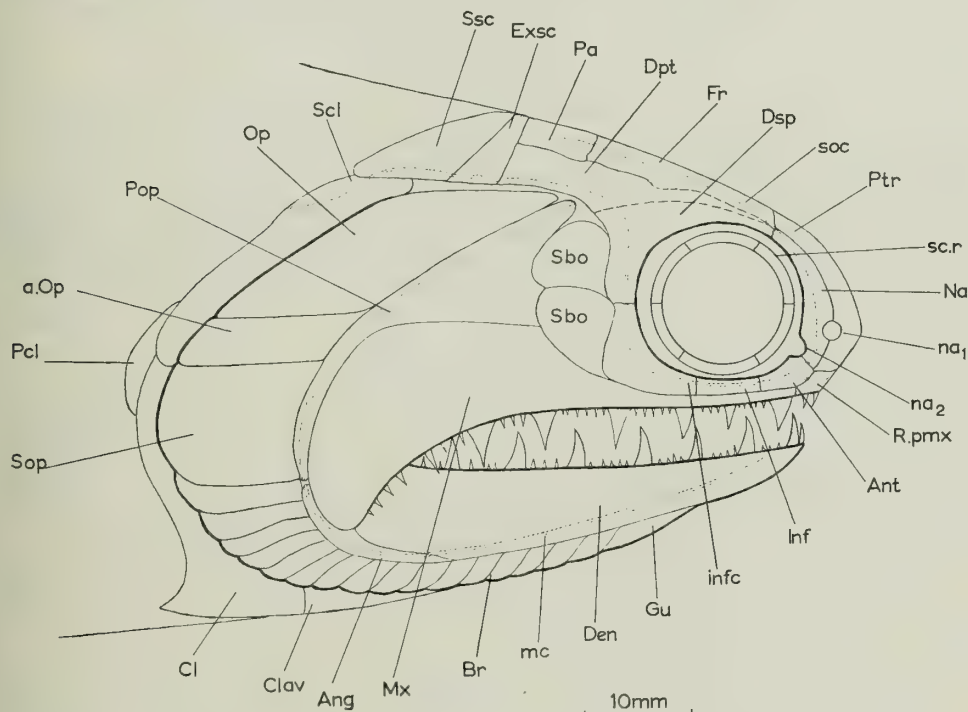


FIG. 9. *Rhabdolepis macropterus* (Bronn). Reconstruction of skull in lateral view.

The skull itself is long with an oblique suspensorium and the orbit situated well forwards. The single pair of triangular suprascapulars meet in the midline and are preceded by the normal pair of extrascapulars. The parietals are square and the frontals rectangular. Anteriorly the frontals join the postrostral and the nasals. The lateral wall of the skull is made up of the dermopterotic and the dermosphenotic, but this area is badly preserved in all the specimens I have examined and thus the true extent of these two bones can only be guessed at. Ventrally the nasal joins



the antorbital. This latter bone forms the lower edge of the posterior nostril (see B.M.N.H., P.992). Anterior to the antorbital and beneath the postrostral lies a pair of small rostro-premaxillaries. The rostro-premaxillary is not often observed but it can be seen displaced in front of the snout in specimen B.M.N.H., P.993, where it bears several small pointed teeth. Between the antorbital and the dermosphenotic are two members of the infraorbital series, the posterior one being much the larger. The maxilla is long and narrow and bears teeth along the whole of its ventral margin. These teeth are in two series, a set of very large, pointed teeth and a series of far more numerous, much smaller ones. The preopercular is high and broad and anteriorly the margin is twice scalloped out for the reception of the two suborbital bones. The opercular apparatus is narrow and the accessory opercular completely separates the opercular from the subopercular. There are about sixteen branchiostegal rays and a small lozenge-shaped median gular. The orbit contains a delicate sclerotic ring composed of six segments (see B.M.N.H., P.6196).

*Lower jaw.* The lower jaw is made up of a stout angular posteriorly and with a large dentary forming the remainder of the outer surface. The dentary also forms part of the inner jaw surface anteriorly. The remainder of the inner surface is covered by a large prearticular. The upper border of the dentary supports a series of very large conical pointed teeth and an outer row of numerous, closely arranged, small teeth. These are set on a shelf which is overlapped by the coronoid. The tooth bearing surface of the jaw is almost flat, and posteriorly the articular portion of Meckel's cartilage is ossified.

*Palate.* Little could be made out of the palate apart from there being an ossified quadratojugal bone present, which enters partly into the jaw articulation.

*The paired fins and their girdles.* The pectoral girdle is of the normal palaeoniscoid pattern and contains a single postcleithrum. The dermal bones are delicately ornamented with short striae which run along the length of the bones. There are ossified radials, four or five in number, and the lepidotrichia of the fin number between twenty and twenty-five. All the rays are articulated to their bases.

The pelvic fin is smaller than the pectoral and is composed of fifteen to twenty rays. Both the pectorals and pelvics are fringed anteriorly with very small fulcral scales.

*The unpaired fins.* The dorsal and anal fins are large, distinctly triangular, and concave posteriorly. The dorsal fin is the smaller of the two with from thirty-eight to forty rays, while the anal has between forty-five and fifty lepidotrichia. However, there seems to be considerable variability in numbers of fin rays within this species. The caudal fin is heterocercal, deeply cleft and nearly equilobate.

The endoskeleton of the dorsal fin consists of about seventeen radials, each composed of two separate ossifications, an axonost and a baseost. The baseosts can clearly be seen on B.M.N.H., P.14537 and P.993a; they are hour-glass shaped and diminish gradually in size from before backwards. These baseosts are much larger than those in *Nematoptychius greenocki* (Traquair). The axonosts are much longer and appear to be continuous with the neural spines.



The exoskeleton of the anal fin is also often preserved. It consists of about fifteen radials and although it could not be verified it would appear that these radials consist of two ossifications (B.M.N.H., P.15098), a long axonost and a much shorter hour-glass shaped baseost (B.M.N.H., P.6196).

*Squamation.* The scales are relatively small and about as broad as they are deep on the flank. They are delicately ornamented with oblique striae, which cross the scale surface from the antero-superior corner to the postero-inferior corner. These striae occasionally anastomose, and they finish as a series of digitations on the anterior overlapped border. On the flank scales three or four of these striae at the anterior border run almost parallel to that border.

***Rhabdolepis saarbrueckensis* n. sp.**

(Text-fig. 10)

1891 *Elonichthys macropterus* (Bronn) : Woodward, p. 493.

**DIAGNOSIS.** A species closely resembling the type species except that there are two accessory opercular bones separating the opercular from the subopercular (Text-fig. 10). Probably four ridge-scales in front of dorsal fin and not three as in *Rhabdolepis macropterus* (Bronn).

**HOLOTYPE.** B.M.N.H., 32576 in counterpart, from the Lower Permian of Saarbrück. The only specimen seen.

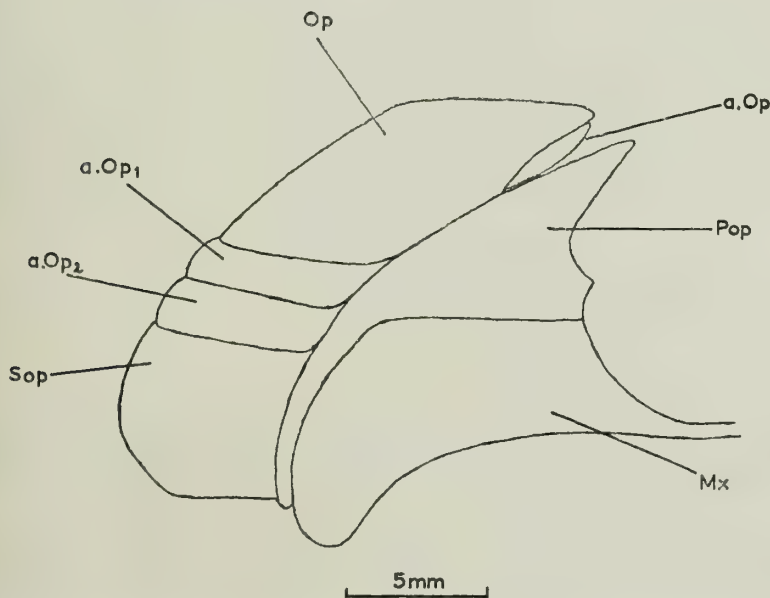


FIG. 10. *Rhabdolepis saarbrueckensis* n. sp. Cheek and opercular apparatus, lateral view.



REMARKS. Woodward (1891 : 493) lists specimen No. 32576 under *Elonichthys macropterus* (Bronn) ; however from the facts given above it clearly belongs to a separate species which I have called *saarbrueeckensis* after the locality where it was found.

DESCRIPTION. This species only differs from the type in the points already cited of which the most significant is the presence of a second accessory opercular bone (a.Op.<sub>2</sub>, Text-fig. 10) lying immediately beneath the first accessory opercular bone.

### Family **AMBLYPTERIDAE** Romer

1954 Romer, p. 579 (name only).

DIAGNOSIS (emended). Trunk deeply fusiform ; dorsal fin partly in advance of, partly opposing, anal fin ; both large, triangular and approximately same size. Dorsal contour much arched in advance of dorsal fin. Paired fins large or of moderate size. All fins with fulcra anteriorly and with rays articulated and distally bifurcating. Suspensorium almost vertical, rostrum only feebly developed if at all. Opercular larger than subopercular. Dermohyal and suborbital series present, branchiostegal rays few and teeth minute.

REMARKS. I have used this family to include the genus *Amblypterus*, but it would seem that the two genera, *Paramblypterus* Sauvage and *Amblypterygia* Berg also belong to this family (as already suggested by Romer, 1945 : 579). Since this paper was written, due to the kindness of Professor J. P. Lehman I have been allowed to read an as yet unpublished thesis entitled : *Étude des Palaeoniscidés du Bassin Houiller de Commentry (Allier)* by Jacques Blot. This has further confirmed my belief that *Paramblypterus* Sauvage [which Blot has shown to include *Amblypterygia* Sauvage, *Geomichthys* Sauvage, *Cosmopoma* Sauvage and *Dipteroma* Sauvage] should be placed in the Amblypteridae, while *Commentrya* Sauvage [shown by Blot to include *Elaveria* Sauvage], which Romer (1945 : 579) also placed in this family, must clearly be removed and put into a family of its own, the Commentryidae, *fam. nov.* (a family fairly close to both the Elonichthyidae and the Amblypteridae).

### Genus **AMBLYPTERUS** Agassiz

1833 *Amblypterus* Agassiz, *partim*, **2**, 1, pp. 4, 37.

1833 *Palaeoniscus* Agassiz, *partim*, **2**, 1, pp. 4, 45, 103.

1873 *Leiolepis* Goldenburg, p. 5 (name only).

1890 *Aedua* Sauvage, p. 16.

1890 *Archeoniscus* Sauvage, p. 19.

DIAGNOSIS (emended). Trunk deeply fusiform ; dorsal fin partly in advance of, partly opposing, anal fin ; both large, triangular and approximately same size. Dorsal contour much arched in advance of dorsal fin. Paired fins large or of moderate size, pelvic pair placed slightly nearer to anal than to pectorals. All fins with minute fulcra anteriorly and with rays articulated and distally bifurcating. Skull with almost vertical suspensorium, slight rostrum and delicate sclerotic ring. Opercular not quite twice as large as subopercular, suborbital series and dermohyal present. Branchiostegal rays few, skull roofing bones coarsely striated. Teeth



minute and in one series. Scales large and smooth except sometimes in anterior abdominal region and immediately behind ventral portion of pectoral girdle where they exhibit a few delicate striae.

TYPE SPECIES. *Amblypterus latus* Agassiz.

REMARKS. As already pointed out under remarks on the genus *Rhabdolepis* (p. 284), Agassiz (1833 : 4) in erecting the genus *Amblypterus* listed several species without designating any one as the type species. Troschel (1857 : 18) later removed several of these species and put them in the new genus *Rhabdolepis*. However, from the remaining species Sauvage (1888 : 58) subsequently correctly designated *Amblypterus latus* Agassiz as the type species of the genus *Amblypterus*. Woodward (1891 : 437) also came to this conclusion, but for somewhat different reasons.

### *Amblypterus latus* Agassiz

(Text-fig. 11)

1833 *Amblypterus latus* Agassiz, **2**, 1, pp. 4, 37, pl. 4, figs. 2-6.

1833 *Amblypterus lateralis* Agassiz, **2**, 1, pp. 4, 39, pl. 4, figs. 1, 7-9.

1857 *Amblypterus latus* Agassiz : Troschel, p. 13, pl. 2, fig. 17.

1877b *Amblypterus latus* Agassiz : Traquair, p. 552.

1877b *Amblypterus lateralis* Agassiz : Traquair, p. 552.

1877c *Amblypterus latus* Agassiz : Traquair, pl. 2, fig. 1.

1888 *Amblypterus latus* Agassiz : Sauvage, p. 58.

1891 *Amblypterus latus* Agassiz : Woodward, p. 437.

1925 *Amblypterus* sp., Watson, p. 824, text-fig. 4.

1937 *Amblypterus latus* Agassiz : Aldinger, p. 217, text-fig. 57.

DIAGNOSIS (emended). A species reaching 20 cm. in total length. Length of head contained about four times in total body length and over one and a half times in maximum depth of trunk. Both dorsal and anal fins large, longer than deep and origin of dorsal behind middle point of back. Anal fin opposed to hinder two-thirds of dorsal. Paired fins also large, pelvic pair smaller than pectoral. Scales large and smooth, caudal pedicle short and robust. Three large ridge scales in front of dorsal fin, two in front of anal fin and three in front of caudal. Dorsal ridge scales extend back from tail almost to dorsal fin.

HOLOTYPE. Part and counterpart of a nearly complete fish in the Strassburg Museum, figured by Agassiz (1833, text-figs. 2, 3) from the Lower Permian of Saarbrück, Germany.

MATERIAL. Specimens from the British Museum (Natural History). Eighteen specimens examined.

REMARKS. A redescription of the type species of the genus *Amblypterus* (*A. latus*) is given below so that the many species which have been placed in this genus by a number of workers may now be more satisfactorily compared.

DESCRIPTION. *The skull*. The general shape of the skull can be seen from Text-fig. 11. The snout is rounded with but a slight protuberance which is nothing like the rostrum seen in *Elonichthys* Giebel or even as marked as in *Rhabdolepis* Troschel. The roofing bones of the skull are ornamented with coarse tubercles



and ridges of enamel. These ridges are most pronounced on the suprascapulars, extrascapulars, parietals, frontals, dermopterotics, dermosphenotics, nasals and postrostral bones, where they follow the length of the bone. The remaining skull bones are much more delicately ornamented; on the opercular and subopercular and suborbitals delicate striae run concentrically round the bones whilst the maxilla, preopercular, infraorbitals, antorbital, branchiostegal rays and lower jaw are almost smooth.

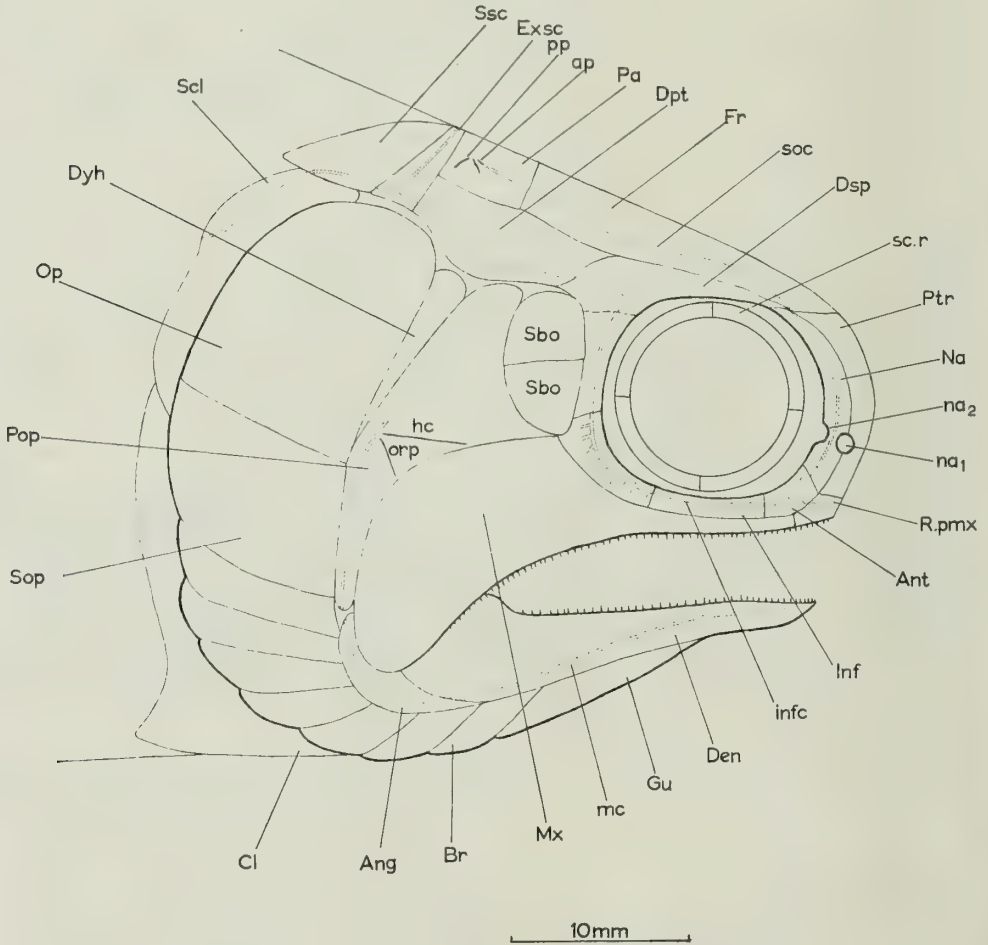


FIG. 11. *Amblypterus latus* Agassiz. Reconstruction of skull in lateral view.

The skull itself is short with an almost vertical suspensorium. The suprascapulars are distinctly triangular and their anterior edge is longer than their lateral border. The extrascapular series consists of the normal single pair of bones and is preceded



by the almost square parietals. The frontals are the longest bones in the skull roof and anteriorly meet both the postrostral and the nasals. The lateral wall of the roof is composed of a dermopterotic which is preceded by a large dermosphenotic. The antero-lateral edge of the dermosphenotic forms part of the upper limit of the orbit, and anteriorly it meets the nasal. Both the postrostral and the nasal bones are long and the postrostral is only moderately convex anteriorly. Ventrally the nasal joins the small antorbital. In front of the maxilla and beneath the postrostral there is evidence of a small rostro-premaxillary (see B.M.N.H., P.145366). There are three members of the infraorbital series and the infraorbital sensory canal gives off numerous, posteriorly directed branches in the second member. The maxilla is of normal palaeoniscoid pattern, but anteriorly the lower margin turns slightly upwards, which, together with the position of the rostro-premaxillary, gives a slight upturning to the snout. The teeth on the maxilla are very small and of one series only. The preopercular is relatively narrow and much nearer the vertical than in any of the other forms so far described in this paper, in fact the preopercular is very similar in shape to that seen in *Mesopoma pulchellum* (Traquair) (Moy-Thomas & Dyne, 1938, text-fig. 9). The anterior margin of the preopercular is convex where the two members of the suborbital series fit into it. Both suborbitals are of roughly the same size and shape. On the preopercular both the vertical and horizontal pit lines can be clearly seen on many of the specimens. Between the preopercular and the opercular is a wedge-shaped dermohyal. The opercular is over one and a half times deeper than the subopercular. Preceding the subopercular are seven broad branchiostegal rays and a large median gular. The orbit is supported by a delicate sclerotic ring, composed probably of four elements; bits of this ring can be seen on specimens B.M.N.H., P.6195a, P.3458a and P.978.

*Lower jaw.* The posterior third of the lower jaw is over twice as deep as the remainder. Anteriorly the jaw is very shallow. The angular bone does not extend very far along the ventral jaw surface and only the articular region of Meckel's cartilage is ossified. The dentary, where it turns under and up to form part of the inner surface of the jaw, is considerably thickened, giving a very stout keel to the lower inner surface. There are three members of the coronoid series, all of which bear small tubercles on their dorsal surface. The lower jaw is well shown on B.M.N.H., 44082 and on one specimen of *Amblypterus duvernoyi* (Agassiz) B.M.N.H., P.21987 which is very similar to *A. latus*.

*The paired fins and their girdles.* The pectoral girdle consists of a supracleithrum which stretches down to beyond the junction of the opercular and subopercular, an elongate cleithrum and a stout clavicle. The ornamentation is more pronounced on the supracleithrum and cleithrum than on the opercular series. It consists of elongate striae of enamel which follow more or less the long axis of the bone. The pectoral fin is large, with a longish base line; there are four or more ossified radials present and the lepidotrichia of the fin number between twenty-five and twenty-eight. All the rays are articulated to their bases.

The pelvic fin is also large, a little smaller than the pectoral, having some twenty lepidotrichia. The base line is long and the rays in the middle region of the fin are



very stout. Both the paired and unpaired fins are fringed anteriorly with small fulcral scales.

*The unpaired fins.* The dorsal and anal fins are large, triangular and, contrary to Woodward (1891 : 438), deeper than they are long. Both fins are of comparable size with twenty-eight to thirty-two lepidotrichia. The tail is heterocercal, deeply cleft and inequilateral.

*Squamation.* The scales are large and smooth, those in the middle of the flank not much deeper than broad.

### Family **STEGOTRACHELIDAE** nov.

**DIAGNOSIS.** Trunk deeply fusiform ; mandibular suspension moderately oblique to oblique ; caudal pedicle robust ; maximum depth of body contained about four times in total length. Dorsal and anal fins opposing one another, caudal fin heterocercal. Prominent dorsal and ventral ridge scales in at least the Devonian members. Paired fins small with intervals between articulations in lepidotrichia long. Snout with poorly developed rostrum, generally composed of three bones only, median postrostral, paired nasals and rostro-premaxillo-antorbital. Frontals nearly always pierced by pineal foramen. Ornamentation of skull roofing bones consisting of fine ridges of enamel which follow the length of the bones. Scales ornamented with diagonal ridges which often end on posterior scale margins as series of serrations.

**REMARKS.** I have erected this family to include the two Devonian genera *Stegotrachelus* (Woodward & White, 1926) and *Moythomasia* (Gross, 1942, 1953), and the Lower Carboniferous genus *Kentuckia* (Rayner, 1951).

Gross (1933b, 1942) has suggested that *Stegotrachelus* is congeneric with *Moythomasia* although Rayner (1951 : 55) thinks this unlikely. From the following description of *Stegotrachelus* it is clear that the two genera are quite separate, but on the other hand are close enough to be grouped in the same family.

Rayner (1951 : 54, 75) has shown that *Kentuckia* is also closely related to *Moythomasia* and as such it too may be included in the family Stegotrachelidae.

### Genus **STEGOTRACHELUS** Woodward & White, 1926

**DIAGNOSIS.** See Woodward & White, 1926 : 567.

**TYPE SPECIES.** *Stegotrachelus finlayi* Woodward & White.

**REMARKS.** Since Gross (1942) has suggested that *Stegotrachelus* is congeneric with *Moythomasia* a re-examination of *Stegotrachelus* can profitably be undertaken. Of the six Devonian genera of actinopterygians so far described *Cheirolepis* Agassiz, *Tegeolepis* Miller, *Stegotrachelus* Woodward & White, *Moythomasia* Gross, *Osorioichthys* Casier and *Orvikuina* Gross, two are known only by scales and of the remainder only the skulls of *Cheirolepis* Agassiz and *Moythomasia* are at all well known.



***Stegotrachelus finlayi* Woodward & White**  
(Text-fig. 12)

1926 *Stegotrachelus finlayi* Woodward & White, p. 568, pl. 3.

1937 *Stegotrachelus finlayi* Woodward & White : Aldinger, p. 298, text-fig. 90.

DIAGNOSIS. See Woodward & White (1926 : 567) with the following emendments :—(1) There is no suborbital series present. (2) The frontal is pierced by a pineal foramen. (3) The snout has a slight rostrum and is composed of three bones only, median postrostral, paired nasals and rostro-premaxillo-antorbitals.

HOLOTYPE. Nearly complete fish (B.M.N.H., P.13407) from the Middle Old Red Sandstone of Exnaboe, Shetland.

MATERIAL. Specimens from the British Museum (Natural History) (including the type) and from the Royal Scottish Museum. Twelve specimens in all.

REMARKS. This is the only species of this genus so far described. The general form of the body and fins have been well described and figured by Woodward & White (1926 : 568) but a more detailed study of the head is clearly needed. In the last few years new material of *Stegotrachelus finlayi* has been collected by Mr. H. Crawford and presented to the British Museum (Natural History) and this, together with the old material, has made the following description possible.

DESCRIPTION. *The skull.* The skull roofing bones are well shown in B.M.N.H., P.13410, P.20309 and P.45056. The suprascapular series consist of a single pair of bones which are large, triangular, and can be seen displaced in B.M.N.H., P.13413. The extrascapular series is made up of a single pair of very narrow bones much as in *Moythomasia nitida* Gross, but the square parietals succeeding them are smaller by comparison than those in *Moythomasia*. The frontals can clearly be seen in B.M.N.H., P.13410, P.20309 and P.45056, where they are pierced anteriorly by a large pineal foramen as in *Moythomasia perforata* (Gross). The lateral wall of the skull roof is composed of the dermosphenotic and dermopterotic. The dermosphenotic lies anteriorly to the dermopterotic (see B.M.N.H., P.13410 and P.45056), as in *Moythomasia perforata* and *Kentuckia deani* (Eastman), and it does not take part in the formation of the orbital border. Anteriorly the dermosphenotic joins the nasal.

The postrostral has a broad "V"-shaped insertion between the anterior extremities of the frontals, just anterior to the pineal foramen, again a very similar condition is seen in *Moythomasia perforata* (B.M.N.H., P.20309 for the anterior extremities of the frontals and P.13410 for the postrostral). The postrostral is long and the nasals which lie alongside it are of about the same length. The nasals are notched for the anterior and posterior nostrils, these notches being clearly observable on B.M.N.H., P.20310. The bone lying along the posterior margin of the nasal in P.13410 is the displaced nasal from the other side, not a circumorbital as figured by Woodward & White (1926, text-fig. 7, pl. 3, fig. 5). The postrostral curves sharply just at the point where the nares open on to the external surface (see B.M.N.H., P.20310). Beneath the postrostral and nasals lie the paired rostro-



premaxillo-antorbital. The rostro-premaxillo-antorbital bears teeth along its ventral margin and although fragmentary can just be made out on B.M.N.H., P.13410 and P.13407.

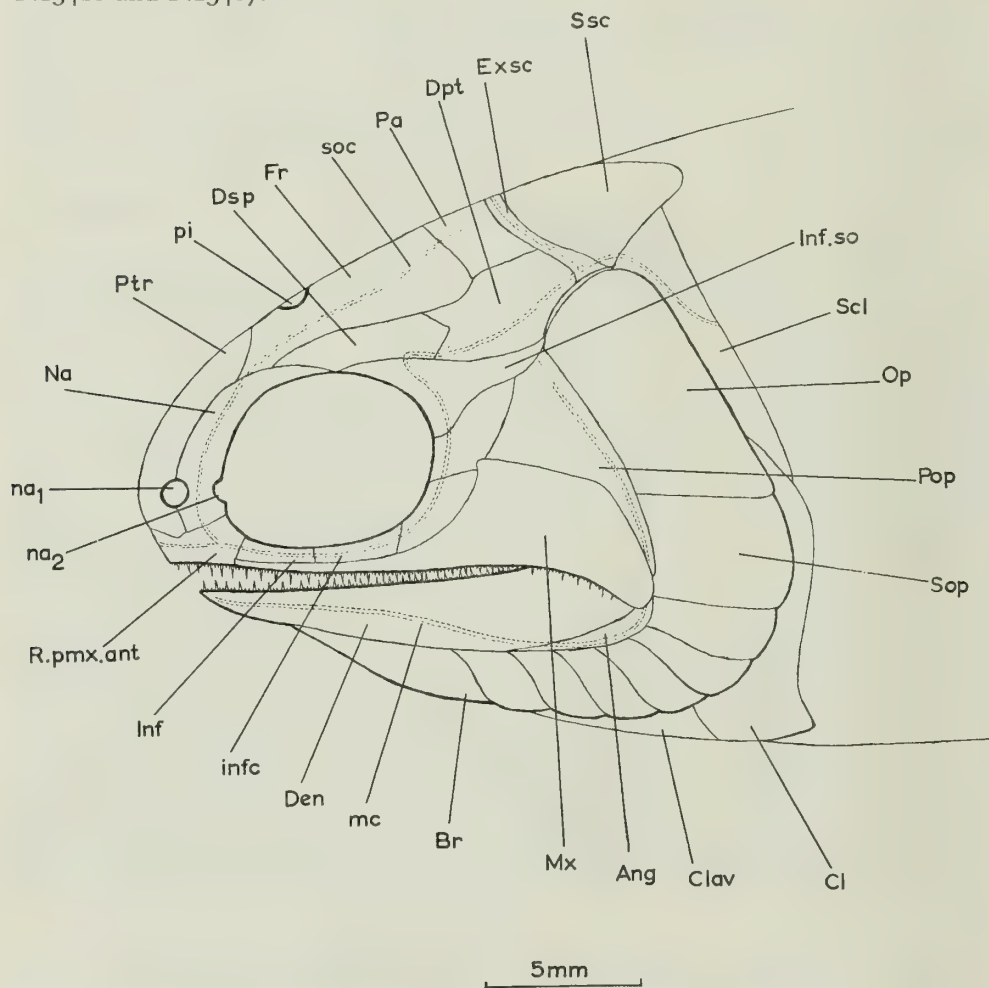


FIG. 12. *Stegotrachelus finlayi* Woodward & White. Reconstruction of skull in lateral view.

Bounding the orbit below and behind are four members of the infraorbital series, the fourth, the most dorsal member being the largest (B.M.N.H., P.13407, P.13410 and P.13416). Dorsally the fourth infraorbital meets the infraorbito-supraorbital (B.M.N.H., P.13410 and P.13416). The infraorbito-supraorbital posteriorly meets the preopercular, dorsally both the dermopterotic and dermosphenotic and anteriorly the nasal. It is the same bone as that called postorbital by Rayner (1951, text-fig. 2) in *Kentuckia deani* and that labelled postfrontal in *Cheirolepis trailli* Agassiz (Watson,



1925 : 817), as Rayner (1951 : 57) has already pointed out. A similar bone is also found in *Nematoptychius greenocki* (Text-fig. 5).

The maxilla is of the normal palaeoniscoid pattern and bears a double series of teeth along its entire ventral margin. The teeth are delicate and there is a series of larger teeth interspersed with a series of more numerous, much smaller teeth. The preopercular (B.M.N.H., P.13410, P.13407 and P.13409) is of rather unusual shape in so much as its dorsal extremity is notched for the reception of the posterior end of the infraorbito-suborbital. The opercular is nearly upright, over twice as high as it is broad and over twice as high as the subopercular. The branchiostegal rays are few in number (seven) and the most anterior pair are very large.

*Lower jaw.* The lower jaw is composed of a long dentary bone which forms almost all of the outer jaw surface, with the posterior jaw margin made up of a narrow angular. The dentary also forms almost the whole of the inner jaw surface anteriorly and is overlain by a long flat prearticular. The articular region of Meckel's cartilage is ossified and so too is the following third. Whether or not other elements such as coronoids and surangular existed could not be ascertained. The dentary, like the maxilla, bears a large number of teeth of two sizes. Of the other skull bones, palate, neurocranium, etc., little could be made out.

REMARKS. The Upper Devonian of North America has yielded the following palaeoniscoid species :— *Palaeoniscus devonicus* Clarke, *Palaeoniscus reticulatus* Williams, *Palaeoniscus antiquus* Williams and *Actinophorus clarki* Newberry. These were all described prior to 1900 and since that time only Hussakof & Bryant (1918) and Gross (1933, 1953) appear to have more than just mentioned any of them. As Devonian forms they are obviously of considerable importance, thus I am describing them below in their appropriate genera. The first three species, *P. devonicus* Clarke, *P. reticulatus* Williams and *P. antiquus* Williams belong to the genus *Moythomasia* Gross but the fourth, *A. clarki* Newberry, belongs to a separate genus and family (Tegeolepididae).

### Genus *MOYTHOMASIA* Gross, 1950

1942 *Aldingeria* Gross, p. 431.

DIAGNOSIS. See Gross, 1942 : 430.

TYPE SPECIES. *Moythomasia perforata* (Gross).

### *Moythomasia devonica* (Clarke)

1879 *Palaeoniscus* sp., Hinde, p. 353.

1885 *Palaeoniscus devonicus* Clarke, pp. 20, 41, pl. 1, figs. 2-6.

1886 *Palaeoniscus reticulatus* Williams, pp. 82, 83, fig. 1a, e.

1891 *Palaeoniscus devonicus* Clarke : Woodward, p. 485.

1891 *Palaeoniscus reticulatus* Williams : Woodward, p. 485.

1918 *Rhadinichthys devonicus* (Clarke) = *Rhadinichthys reticulatus* (Williams) : Hussakof & Bryant, p. 182, pls. 59-61, pl. 63, figs. 1, 2, pl. 65, text-figs. 60, 61.

1926 *Rhadinichthys devonicus* (Clarke) : Woodward & White, p. 570.



- 1932 *Palaeoniscus devonicus* Clarke : Woodward, p. 117.  
 1933a *Rhadinichthys devonicus* (Clarke) : Gross, p. 59.  
 1933b *Rhadinichthys devonicus* (Clarke) : Gross, p. 71.  
 1937 *Rhadinichthys devonicus* (Clarke) : Aldinger, p. 204 (name only).  
 1953 *Rhadinichthys devonicus* (Clarke) : Gross, p. 85 (name only).  
 1958 "*Rhadinichthys* " *devonicus* (Clarke) : Lehman, p. 2136 (name only).  
 1958 "*Rhadinichthys* " *reticulatus* (Williams) : Lehman, p. 2136 (name only).

DIAGNOSIS (emended). A species reaching a length of 13 cm. Trunk fusiform, elongated ; teeth little larger than those in type species. Bases of teeth on maxilla fused to surrounding bone. Posterior margins of joints of some lepidotrichia delicately denticulated [as in *Elonichthys robisoni* (Hibbert)]. See also Clarke, 1855 : 20, 41 and Hussakof & Bryant, 1918 : 182.

HOLOTYPE. Isolated bones and scales at one time in the Buffalo Museum, from Portage, Ohio and Genesee Shales, New York State.

MATERIAL. Specimens from the British Museum (Natural History). About ten specimens, consisting mainly of scales were examined.

REMARKS. Woodward (1932 : 117) considered *Palaeoniscus devonicus* Clarke to be very similar to *Stegotrachelus finlayi* Woodward & White, but later Gross (1933, 1942), after a comparison of their scales, came to the conclusion that *Rhadinichthys devonicus* (Clarke) should be placed in the genus *Moythomasia*. This is further borne out by a comparison of the text-figures and plates of *Rhadinichthys devonicus* (Clarke) given in Hussakof & Bryant (1918) and the illustrations of *Moythomasia nitida* Gross given in Gross (1953, pl. 4). The maxillae of these two species are very similar, both having the same general proportions and both possessing a slight concavity in their dorsal margins. This maxilla is not at all like that described in *Stegotrachelus finlayi* Woodward & White (Text-fig. 12). The opercular of *Rhadinichthys devonicus* (Clarke) also bears a close resemblance to that seen in *Moythomasia nitida* Gross and finally both the scales and the skull roofing bones are similarly ornamented in the two species. Thus I feel there is every justification for placing *Palaeoniscus devonicus* Clarke (1885) in the genus *Moythomasia*.

### ***Moythomasia antiqua* (Williams)**

- 1886 *Palaeoniscus antiquus* Williams, pp. 82, 84, fig. IIa, d.  
 1891 *Palaeoniscus antiquus* Williams : Woodward, p. 485.  
 1918 *Rhadinichthys antiquus* (Williams) Hussakof & Bryant, p. 186, pl. 63, fig. 3, pl. 64, text-fig. 62.  
 1933b *Rhadinichthys antiquus* (Williams) : Gross, p. 72.  
 1953 *Rhadinichthys antiquus* (Williams) : Gross, p. 85 (name only).  
 1958 "*Rhadinichthys* " *antiquus* (Williams) : Lehman, p. 2136 (name only).

DIAGNOSIS. See Williams, 1866 : 82, 84, figs. 2a, d.

HOLOTYPE. Isolated scales, at one time in the Buffalo Museum, from the Portage Group, Sturgeon Point, Erie County, New York.



REMARKS. This species is known only from isolated scales, but as Gross (1933*b*, 1953) has pointed out, they bear a close resemblance to *Moythomasia laevigata* Gross. Although I am loth to accept species based only on scales, for the sake of completeness of the record, I think that they are sufficiently different from the scales of *Moythomasia devonica* (Clarke) and from any of the other species of *Moythomasia* described by Gross (1933*a*, 1933*b*, 1953) to warrant a separate species for their reception.

Family **TEGEOLEPIDAE** Romer, 1945 : 579 (name only)

DIAGNOSIS. Trunk elongated, body cylindrical, skull pointed anteriorly. Fins, apart from caudal, without fulcra, delicate and many rayed. Caudal fin strongly heterocercal, pectoral fin-rays unarticulated, but distally bifurcated. Branchiostegal rays numerous, teeth acutely conical and arranged in two series -an inner row of well spaced, large laniaries and an outer row of numerous, small, closely arranged teeth. Scales where present, rhomboidal, small, narrow and very thin.

REMARKS. I have used this family to include the Upper Devonian genus *Tegeolepis*, but the Triassic genus *Apateolepis* Woodward from the Hawkesbury Beds of New South Wales also appears to be a late relic of this family.

The Tegeolepidae occupy an intermediate position between the Palaeonisciformes on the one hand and the Chondrosteiformes on the other (see remarks on *Tegeolepis clarki*).

Genus **TEGEOLEPIS** Miller, 1892

1888 *Actinophorus* Newberry, p. 179.

DIAGNOSIS (emended). Trunk elongated ; body cylindrical, skull pointed anteriorly. Fins, apart from caudal, without fulcra, delicate and many rayed ; caudal fin deeply cleft, pectoral fin-rays unarticulated but distally bifurcated. Skull with strongly developed rostrum, postrostral very long and rostro-premaxillo-antorbital without teeth. Maxilla well developed and subopercular of normal palaeoniscoid proportions. Suprascapular very large and extrascapular series composed of four or more bones. Lateral skull wall with well developed infraorbito-supraorbital bone, and dermopterotic extending a considerable distance behind parietals. Gulars numerous, teeth consisting of well-formed, conical laniaries and numerous smaller teeth ; scales rhomboidal, small, narrow and very thin ; scale covering complete.

TYPE SPECIES. *Actinophorus clarki* Newberry.

REMARKS. This genus was first described by Newberry (1888) under the name *Actinophorus*, but as Miller (1892) pointed out, this genus was already preoccupied by a coleopteran (Creutzer, 1799), and he therefore proposed the new name *Tegeolepis*. Only one species has so far been described.



*Tegeolepis clarki* (Newberry)

(Pls. 1, 2 ; Text-fig. 13)

1888 *Actinophorus clarki* Newberry, p. 179.1890 *Actinophorus clarki* Newberry : Newberry, p. 175, pl. 49, figs. 1, 1a.1891 *Actinophorus clarki* Newberry : Woodward, p. 487.1892 *Tegeolepis clarki* (Newberry) Miller, p. 717.1953 *Tegeolepis clarkii* (Newberry) : Gross, p. 85 (name only).

DIAGNOSIS. A large species reaching almost a metre in length, cranial roof bones and cheek bones ornamented with tubercles and short ridges of enamel.

HOLOTYPE. Fish showing underside of head and pectoral fins, A.M.N.H., No. 230 from the Cleveland Shale, Brooklyn, Cuyahoga County, Ohio (Upper Devonian).

MATERIAL. Specimens from the British Museum (Natural History), latex peels of the holotype and of a second specimen in the American Museum of Natural History, New York. Four specimens were examined.

REMARKS. This species shows many similarities to members of the Chondrosteiformes. The scales are very thin and small in *Tegeolepis clarki* and in this show a condition which could easily lead to the rudimentary scaling found in the later Chondrosteiformes. The pectoral fin devoid of fulcral scales and without articulations in *T. clarki* is again reminiscent of the condition seen in *Chondrosteus* Egerton from the Lias. The pointed snout and well developed rostrum is of the right order to derive not only *Chondrosteus* but even *Palaeopsephurus* MacAlpin. On the other hand, *T. clarki* still has a well developed maxilla of normal palaeoniscoid proportions and a small subopercular. Reduction in the maxilla and enlargement of the subopercular would be necessary before a condition such as that seen in *Chondrosteus* could be achieved. However I have little doubt that the Tegeolepidae were the palaeoniscoid family from which the much later Chondrosteiformes evolved although *Tegeolepis clarki* may not have been the direct ancestor.

DESCRIPTION. *The skull.* The external bones of the skull are delicately ornamented with tubercles and ridges of enamel. On the skull roofing bones the ridges are more pronounced and run along the length of the bones. On the maxilla, infraorbitals, lower jaw and branchiostegal rays the ridges of enamel are finer and not so prominent, intercalating and anastomosing. Superimposed on these ridges are numerous tubercles (see Pl. 2).

The skull of *Tegeolepis clarki* is long with an oblique suspensorium and the orbit situated well forward. The skull roofing bones are only visible on one specimen, A.M.N.H., No. 361, where they have been considerably displaced. The suprascapular is very long (Text-fig. 13), far longer than what is normal in the Palaeonisciformes. In this respect it is very similar to that seen in *Chondrosteus acipenseroides* Egerton, *Chondrosteus hindenburgi* Pompeckj and *Birgeria groenlandica* Stensiö. The extrascapular series appears to be made up of at least four bones (cf. *Acipenser sturio* L.), a pair of small central members, which anteriorly meet the two parietals and two larger bones, one on either side of this median pair which laterally join the dermopterotics.



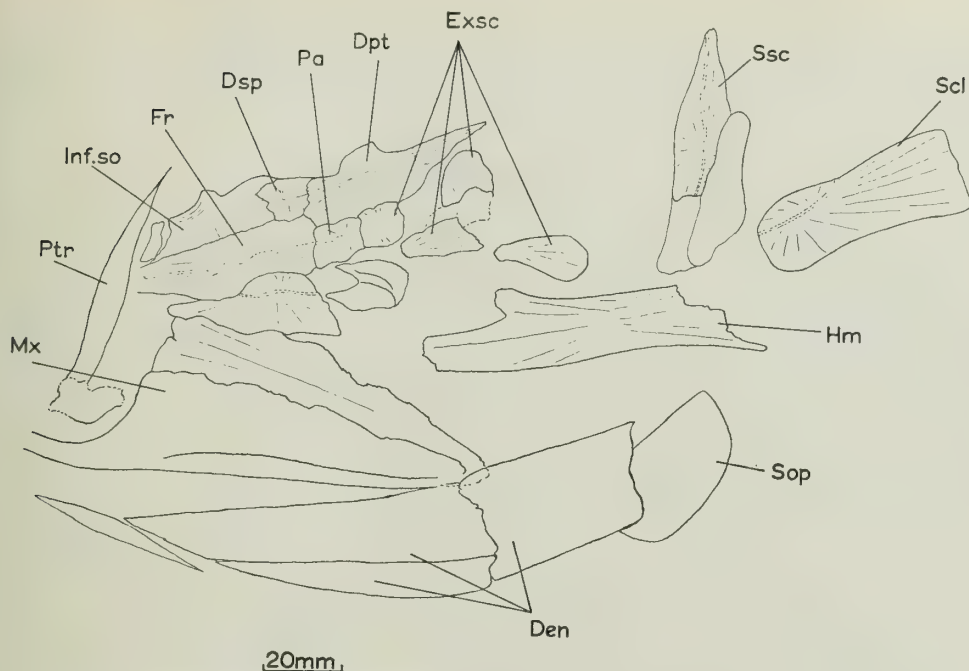


FIG. 13. *Tegeolepis clarki* (Newberry). Sketch of the skull bones on specimen A.M.N.H. 361.

The parietals are small and square in outline and are preceded by a single pair of long frontals. Anteriorly the frontals join the long postrostral. The postrostral from what I can deduce is a single bone which is responsible for the long pointed extension to the head. Anteriorly it is strongly elbowed much as in *Elonichthys serratus* Traquair (Moy-Thomas & Dyne, 1938 : 22). Ventrally the postrostral meets the paired rostro-premaxillo-antorbital. The rostro-premaxillo-antorbital does not bear teeth and can be seen on A.M.N.H. No. 230 (the holotype) anterior to the limits of the lower jaw.

The lateral wall of the skull roof is composed of three bones, the dermopterotic, dermosphenotic and the infraorbito-supraorbital (A.M.N.H., No. 361). The dermopterotic like the suprascapular is a long bone extending posteriorly beyond the limit of the extrascapular series. Anteriorly it makes contact with the frontal and the dermosphenotic, laterally it bounds the extrascapulars and the parietal. The dermopterotic both in shape and position is very similar to that seen in a specimen of *Chondrosteus hindenburgi* Pompeckj (Hennig, 1925) in the Tübingen Museum, and to *Birgeria groenlandica* Stensiö (Nielsen, 1949). Anterior to the dermopterotic is a small dermosphenotic which anteriorly again joins the infraorbito-supraorbital. The infraorbito-supraorbital is much larger than the dermosphenotic and forms part of the dorsal border of the orbit.

The maxilla is of the normal palaeoniscoid shape, except that its expanded



posterior position is not as high as in most Palaeonisciformes (B.M.N.H., P.45312, Pl. 2). The posterior expanded portion is gently rounded dorsally and the ventral edge of the maxilla turns slightly upwards anteriorly. The maxilla bears a series of stout conical laniaries, interspersed with a series of much smaller, more numerous teeth. The subopercular is not enlarged (Text-fig. 13) as in *Chondrosteus acipenseroides* Egerton but whether a large opercular existed could not be ascertained. The branchiostegal rays numbered thirty or more members.

Of the remaining skull bones little could be made out, but there is some evidence of an infraorbital series bounding the orbit below and behind.

*The Palate.* The palatoquadrate portion of Meckel's cartilage was ossified and its anterior portion can be seen on A.M.N.H., No. 230. The palatoquadrate is also ossified in *Chondrosteus hindenburgi* (see specimen in Tübingen Museum).

The hyomandibular is both wide and relatively straight, and from its position in A.M.N.H., No. 361 the suspensorium must have been very oblique. The hyomandibular bears a distinct opercular process so that I conclude that a large opercular was probably present. The size, shape and position of the hyomandibular is very reminiscent of the condition seen in the Recent *Polydon*.

*Lower jaw.* The outer surface of the lower jaw is composed of three bones (see B.M.N.H., P.45312). The posterior margin is made up of a stout angular which is preceded antero-dorsally by the surangular. The remainder of the outer surface is made up of the dentary. The disposition of the bones in the lower jaw is very similar to that seen in *Birgeria groenlandica* Stensiö (Nielsen, 1949).

*The paired fins and their girdles.* The supracleithrum is large and broad and can be seen displaced in A.M.N.H., No. 361. The cleithrum was not recognisable on any of the specimens.

The pectoral fin has from sixty-five to seventy rays, the first six of which are the stoutest and the sixth, seventh and eighth the longest. The rays are smooth, distally bifurcated and unarticulated (see B.M.N.H., P.9402).

No specimen shows the pelvic fin but in B.M.N.H., P.9402 (Pl. 1, Pv) part of the endoskeleton of the fin is preserved. The pelvic plate of each fin is slightly concave towards the midline while its lateral border is slightly convex. Posteriorly the plate is expanded and presumably a series of radials were supported at this point. An ossified pelvic plate has been described in *Birgeria mougeoti* Agassiz (Stensiö, 1921 : 192) from the Trias.

*The unpaired fins.* The anal fin, although not present on any of the specimens I have examined, was mentioned by Newberry (1880 : 179) as being small and triangular in outline. However, on B.M.N.H., P.9402 two of the supporting axonosts of the anal fin are visible. These axonosts (Ax) are long and expanded ventrally, and are similar in size and shape to those seen in *Chondrosteus acipenseroides*. The caudal is strongly heterocercal, the dorsal fin unknown.

*Squamation.* The scales are quadrangular, very small and narrow, thin and delicate.

REMARKS. Returning to the Middle Devonian of Europe, in particular the Middle Old Red Sandstone of Scotland, very abundant remains of the palaeoniscoid



*Cheirolepis trailli* Agassiz have been found. In order to elucidate the problem of the homologies of the snout bones in the actinopterygians (treated in the discussion) this material of *Cheirolepis trailli* was re-examined.

Family **CHEIROLEPIDAE** Pander, 1860 : 69

DIAGNOSIS (emended). Trunk elongated, mandibular suspension oblique. Fins of moderate size and composed of numerous delicate rays, closely articulated and branching distally ; fulcral scales prominent. Pelvic fins with extended base line, dorsal fin scarcely longer than deep, and fin elongated. Anal fin arising anterior to dorsal. Caudal fin heterocercal, inequilobate and only slightly forked. Scales minute, thick, covered with enamel and with an internal boss. Scales not overlapping.

REMARKS. This family includes one genus only, *Cheirolepis*, from the Middle Devonian of Europe and the Upper Devonian of North America. The affinities of this family remain obscure, no later palaeoniscoid family appears to have been derived from it.

Genus **CHEIROLEPIS** Agassiz, 1835

DIAGNOSIS. See Woodward, 1891 : 451.

TYPE SPECIES. *Cheirolepis trailli* Agassiz.

***Cheirolepis trailli* Agassiz**

(Text-fig. 14)

- 1828 "Second Gamrie Ichthyolite" Pentland, p. 364.
- 1835 *Cheirolepis traillii* Agassiz, **2**, 1, p. 130, pl. i.d, pl. i.e, fig. 4.
- 1835 *Cheirolepis uragus* Agassiz, **2**, 1, p. 132, pl. i.e, figs. 1-3.
- 1844 *Cheirolepis cummingiae* Agassiz, **2**, 1, p. 301 (name only).
- 1844 *Cheirolepis cummingiae* Agassiz, p. 45, pl. 12.
- 1848 *Cheirolepis velox* M'Coy, p. 302.
- 1848 *Cheirolepis curtus* M'Coy, p. 302.
- 1848 *Cheirolepis macrocephalus* M'Coy, p. 303.
- 1855 *Cheirolepis curtus* M'Coy : M'Coy, p. 580, pl. 2d, fig. 1.
- 1855 *Cheirolepis macrocephalus* M'Coy : M'Coy, p. 580, pl. 2d, fig. 3.
- 1855 *Cheirolepis traillii* Agassiz : M'Coy, p. 581.
- 1855 *Cheirolepis uragus* Agassiz : M'Coy, p. 581.
- 1855 *Cheirolepis velox* M'Coy : M'Coy, p. 581, pl. 2d, fig. 2.
- 1855 *Cheirolepis uragus* Agassiz : Eichwald, **1**, 2, p. 1575, pl. 57, fig. 21.
- 1860 *Cheirolepis cummingiae* Agassiz : Pander, pl. 8, figs. 1-3, 5.
- 1860 *Cheirolepis trailli* Agassiz : Pander, pl. 8, fig. 4.
- 1860 *Cheirolepis curtus* M'Coy = *Cheirolepis cummingiae* Agassiz : Egerton, p. 123.
- 1860 *Cheirolepis macrocephalus* M'Coy = *Cheirolepis trailli* Agassiz : Egerton, p. 123.
- 1860 *Cheirolepis velox* M'Coy : Egerton, p. 123.
- 1867 *Cheirolepis trailli* Agassiz : Powrie, p. 152.
- 1867 *Cheirolepis cummingiae* Agassiz : Powrie, p. 152.
- 1867 *Cheirolepis velox* M'Coy = *Cheirolepis cummingiae* Agassiz : Powrie, p. 152.



- 1867 *Cheirolepis uragus* Agassiz : Powrie, p. 152.  
 1875a *Cheirolepis cummingiae* Agassiz : Traquair, p. 240, pl. 17.  
 1888 *Cheirolepis trailli* Agassiz : Traquair, p. 517.  
 1890a *Cheirolepis trailli* Agassiz : Traquair, p. 485.  
 1891 *Cheirolepis trailli* Agassiz : Woodward, p. 452.  
 1895 *Cheirolepis trailli* Agassiz : Traquair, p. 250, pl. 3, fig. 4.  
 1907 *Cheirolepis* sp., Goodrich, p. 768, pl. 45, fig. 13.  
 1909 *Cheirolepis* sp., Goodrich, p. 310, text-fig. 288.  
 1925 *Cheirolepis trailli* Agassiz : Watson, p. 816, text-figs. 1-3.  
 1925 *Cheirolepis cummingii* Agassiz : Jaekel, p. 418, text-fig. 10.  
 1927 *Cheirolepis cummingii* Agassiz : Jaekel, p. 931, text-fig. 58.  
 1935 *Cheirolepis trailli* Agassiz : Watson, p. 166, fig. 36.  
 1937 *Cheirolepis trailli* Agassiz : Aldinger, p. 196, text-figs. 50, 51.  
 1947 *Cheirolepis trailli* Agassiz : Gross, pp. 139, 156, text-figs. 24, 27.  
 1947 *Cheirolepis trailli* Agassiz : Lehman, p. 8, pls. 5, 6.  
 1953 *Cheirolepis trailli* Agassiz : Gross, p. 108, text-fig. 10 a, b.

DIAGNOSIS. See Woodward, 1891 : 452 and Watson, 1925 : 816-821, 824.

SYNTYPES. Imperfect fishes ; olim T. S. Traill Collection. Part of the Traill Collection was subsequently deposited in the Bootle Museum, however this did not contain any material of *Cheirolepis* and since it seems probable that it is no longer in existence I propose as the neotype specimen B.M.N.H., 49182, in counterpart, from the Middle Old Red Sandstone, Lethen Bar, Nairnshire, Scotland.

MATERIAL. Specimens from the British Museum (Natural History), the Royal Scottish Museum, the University Museum Cambridge, University College London, the Geological Survey and Museum and D. M. S. Watson's collection. Approximately eighty specimens were examined.

REMARKS. Although *Cheirolepis trailli* has been adequately described there are two points concerning its structure which have aroused much discussion. First, the opercular apparatus with the two bones "X" and "Y" lying between the opercular and the preopercular. The bone "Y" of Watson (1925 : 819) is clearly the dermohyal whilst the bone "X" of Watson (1925 : 819) is undoubtedly an accessory opercular (for a full discussion of this see earlier under *Watsonichthys pectinatus*). Secondly, the snout region ; according to Watson (1925, text-figs 1-3) there are already at this early stage in actinopterygian evolution three distinct pairs of bones making up the snout, the premaxilla, antorbital and rostral. Westoll (1937c : 570) doubts this but does not give any reason for so doing. I have re-examined the snout region of *Cheirolepis trailli* and this is included in the following description. On re-examining the snout region I have come across a very nice specimen of *Cheirolepis trailli* in the Zoology Museum, Cambridge, which shows the skull roof in dorsal view. Since this skull roof differs in one or two important points from the description given by Watson (1925 : 816) it too is included in the following description.

DESCRIPTION. *The skull.* Several specimens including U.M.Z.C. 425 show a different arrangement of the roofing bones from that described by Watson (1925). Anterior to the dermopterotic is a large bone which considerably extends the lateral margin of the skull roof. This bone I have termed the dermosphenotic-infraorbito-



supraorbital (Text-fig. 14). However it would appear that within this genus this bone is a variable character and may either be present as a single ossification (Dsp.Inf.so in Text-fig. 14) or as two independent ossifications (I.tem. and Pt.f, Watson, 1925, text-fig. 1).

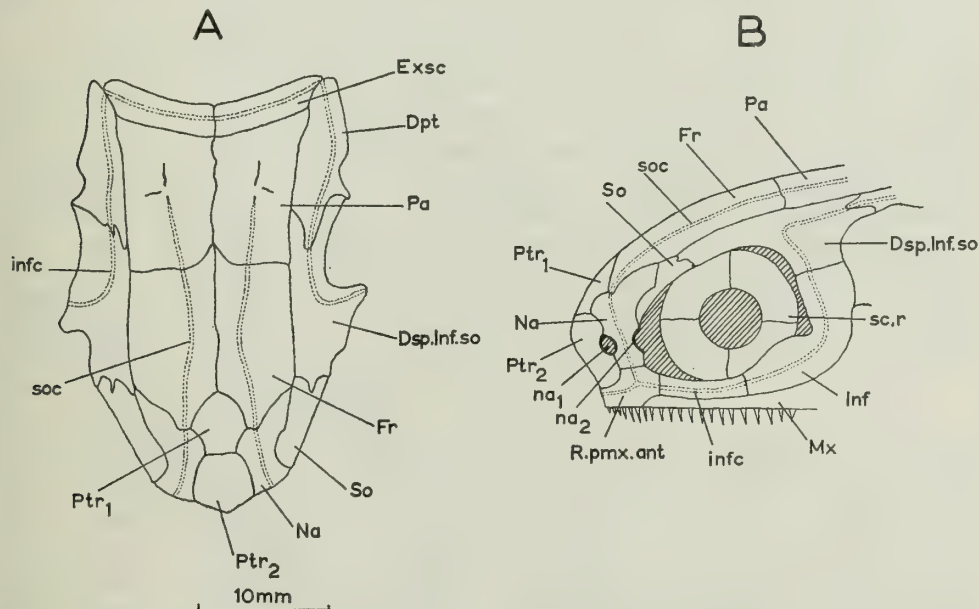


FIG. 14. *Cheirolepis trailli* Agassiz. (a) Reconstruction of skull roof. Mainly from U.M.Z.C. 425. (b) Reconstruction of snout.

The snout region is never very satisfactorily preserved and consequently the interpretation of it is open to question, also there appears to be some variability in the bone arrangement from specimen to specimen. My own interpretation of the snout region is given in Text-fig. 14B, and I believe that there is a single paired ossification ventro-anteriorly, the rostro-premaxillo-antorbital. Evidence of this ossification and of the nasal which lies above it can be seen on B.M.N.H., P.4345 and also on B.M.N.H., 35778 and P.6421. The nasal (B.M.N.H., P.4345) bears two notches, one anteriorly for the anterior nostril (na<sub>1</sub>) and the other posteriorly for the posterior nostril (na<sub>2</sub>). Dorso-posteriorly the nasal joins the supraorbital.

Thus on my interpretation the snout of *Cheirolepis trailli* is very similar to that seen in other primitive palaeoniscoids, in particular *Stegotrachelus finlayi* and *Tegeolepis clarki*. Further, since it seems probable that the primitive actinopterygian snout was composed basically of three bones only, the paired nasals, the paired rostro-premaxillo-antorbitals and a median postrostral (see later under discussion), *Cheirolepis trailli* now fits into place and is no longer an exception to the rule. As a further justification for my reconstruction of the snout region of *Cheirolepis trailli*, I would like to point out that I have not seen an independent rostral element below the parasemionotid level of organization.



*Cheirolepis canadensis* Whiteaves

(Text-fig. 15)

1881 *Cheirolepis canadensis* Whiteaves, p. 33.1889 *Cheirolepis canadensis* Whiteaves : Whiteaves, p. 90, pl. 8.1891 *Cheirolepis canadensis* Whiteaves : Woodward, p. 457.1918 *Cheirolepis canadensis* Whiteaves : Hussakof & Bryant, p. 181, pl. 7 vii, figs. 1, 2.1947 *Cheirolepis canadensis* Whiteaves : Gross, pp. 139, 156, text-figs. 25*b*, 26, 28.1947 *Cheirolepis canadensis* Whiteaves : Lehman, pp. 1-44.1953 *Cheirolepis canadensis* Whiteaves : Gross, pp. 85, 108, text-fig. 10*c*.

DIAGNOSIS. See Woodward, 1891 : 457 and Lehman, 1947 : 1.

HOLOTYPE. Imperfect fish ; Geological Survey of Canada, Ottawa, from Scaumenac Bay, P.Q., Canada (Upper Devonian).

MATERIAL. Specimens from the British Museum (Natural History).

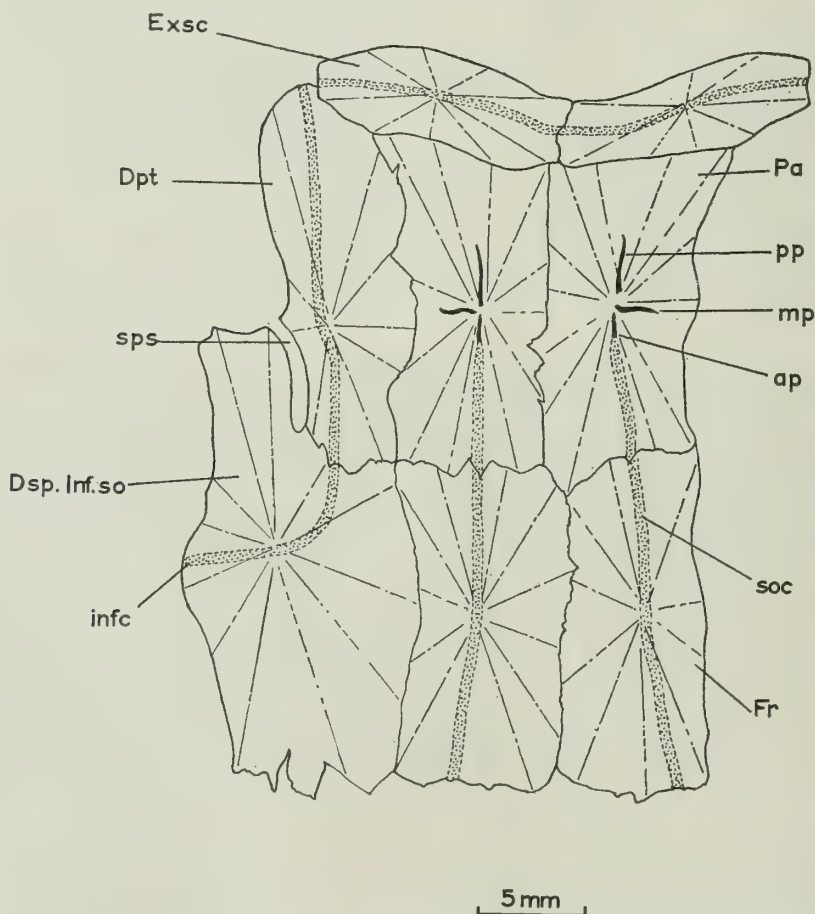


FIG. 15. *Cheirolepis canadensis* Whiteaves. Reconstruction of skull roof. From B.M.N.H., P.6815.



REMARKS. Although this species has been fairly adequately described, the skull roof has not so far been very clearly figured. One specimen, B.M.N.H., P.6815, shows a perfectly preserved skull roof in dorsal view and in order to supplement that description already given for *Cheirolepis trailli* it is described below.

DESCRIPTION. *The skull roof.* The dermal bones of the skull roof and the course of the sensory canals, as far as can be determined, are shown in Text-fig. 15. The parietals and frontals are rectangular and of approximately the same size. The dermopterotic is large and a little longer than the parietal. Anteriorly the dermopterotic joins the very large dermosphenotic-infraorbito-supraorbital. This is a similar ossification to that already described in *Cheirolepis trailli*. One point of difference, however, is that in *Cheirolepis canadensis* it is produced posteriorly to a greater extent and between this posterior projection of the dermosphenotic-infraorbito-supraorbital and the dermopterotic there is a well marked slip (sps). This slit represents the spiracular notch and a similar slit in an almost identical position has been described in *Kentuckia deani* (Eastman) by Rayner (1951 : 57).

### III. DISCUSSION

#### *The snout region in actinopterygians*

The sensory canals in actinopterygians influence the ontogeny of the dermal bones through which they pass (Pehrson, 1922, 1940, 1944a, b). Basically one bone primordium develops in relation to each sensory canal neuromast, thus a series of bone primordia is formed along the length of each sensory canal. The number of bone primordia varies with the number of neuromasts which go to make up any one canal. Thus the number of neuromasts must have been large in acanthodians (Stensiö, 1947, text-fig. 11, B, C) but small in palaeoniscoids, subholosteans and holosteans. Normally these bone primordia fuse together to give the adult sensory canal carrying bones. The adult sensory canal bones then are usually formed from two or more bone primordia which belong to one and the same series. It has been argued by Stensiö (1947) that some sensory canal carrying bones also include, besides the sensory canal elements, anamestic components. The term anamestic was first introduced by Westoll (1937a) and has been used by Stensiö (1947) for the non-sensory line bearing elements of the head in fishes and amphibians. In evidence Stensiö (1947 : 125) quotes such forms as *Amia*, *Acipenser* and teleosts, where he believes that the median dorsal series of anamestic bones have entered into the formation of the frontals and parietals of both sides. In contrast most modern embryologists believe that adult sensory canal bones in both fishes and amphibians are composed exclusively of bone elements developed in relation to sensory canals. Stensiö further believes, and I agree with him entirely, that in certain cases adjoining elements from sensory lines may fuse together, particularly if one of the sensory lines fails to differentiate ; only by this view can the presence of binary bone primordia in relation to certain sensory lines in *Amia* be explained. In other cases Stensiö (1947) believes that sensory lines or parts of them persist even though the underlying bone originally connected with them has disappeared, for example, the anterior division of the supramaxillary line in *Amia* and teleosts.



Finally, Stensiö (1947), in contradistinction to Pehrson (1922, 1940, 1944a, b) and Westoll (1937b, 1940, 1944) believes that the sensory line grooves and pit lines in bony fishes play fundamentally the same part in the embryonic formation of sensory line bones as do the sensory canals proper, and Lekander's later work (1949) on the sensory line system of the Ostariophysi would tend to support Stensiö. Stensiö's case for this point of view is entirely convincing and logical. Thus we see that the dermal bones of the head of bony fishes are referable to two categories, sensory line elements and anamestic elements. The sensory line carrying bones may be formed entirely from sensory line elements or from both sensory line elements and anamestic elements which have fused. The anamestic bones, or "space fillers" as Westoll (1937a) considered them, are a primitive constituent of the dermal skeleton of the head and are, in my opinion, of equal phyletic importance to the sensory canal bones.

From an examination of palaeoniscoids, subholosteans and holosteans it cannot be doubted that in these groups an almost complete series of bones is found in connection with the sensory line canals, grooves and pit lines of the head; further, these sensory canals, grooves and pit lines took an active part in the embryological formation of the associated series of dermal bones and retained their connection with them. In discussing the snout region in actinopterygians it is possible to trace the fates of different dermal bones because of their fixed relationship to the contained sensory canals and to one another.

For some time now the terminology used for the bones in the snout region of palaeoniscoids, subholosteans, holosteans and teleosts has become more and more confused. As a result the rather awkward nomenclature applied to these snout bones has grown up. This nomenclature has been discussed at length by both Nielsen (1942) and Westoll (1944), but without really clarifying the situation. Since many of the palaeoniscoids described in this paper show the snout region particularly well, a reassessment of the situation can usefully be given.

The primitive actinopterygian snout was composed of three bones only, the paired nasals, the paired rostro-premaxillo-antorbital and the single postrostral. This condition can be seen in some Devonian genera such as *Tegeolepis clarki*, *Cheirolepis trailli* (Text-fig. 14) and *Stegotrachelus finlayi* (Text-fig. 12) and is quite common among Carboniferous genera (i.e. *Canobius elegantulus* Text-fig. 16 A, *Rhadinichthys canobiensis* (16B), *Kentuckia deani* (16D), *Paramesolepis tuberculata* (16E), *Pyritoccephalus sculptus* (16G), *Haplolepis tuberculata* (16H)). This condition is still retained by much later palaeoniscoids and subholosteans, as for example *Palaeoniscus freieslebeni*, Text-fig. 16C, from the Upper Permian and *Diaphorognathus gillioti*, Text-fig. 16F, from the Lower Triassic.

Of the three original bones comprising the snout, two are paired, sensory canal bearing elements and the third a single anamestic bone. This single bone occupying a position anterior to the frontals and lying along the midline of the skull is termed the postrostral. The postrostral never carries a branch of the sensory canal system and is normally bounded on either side by the nasals. Frequently, though not invariably (see later under movement of nares), the postrostral forms the lateral



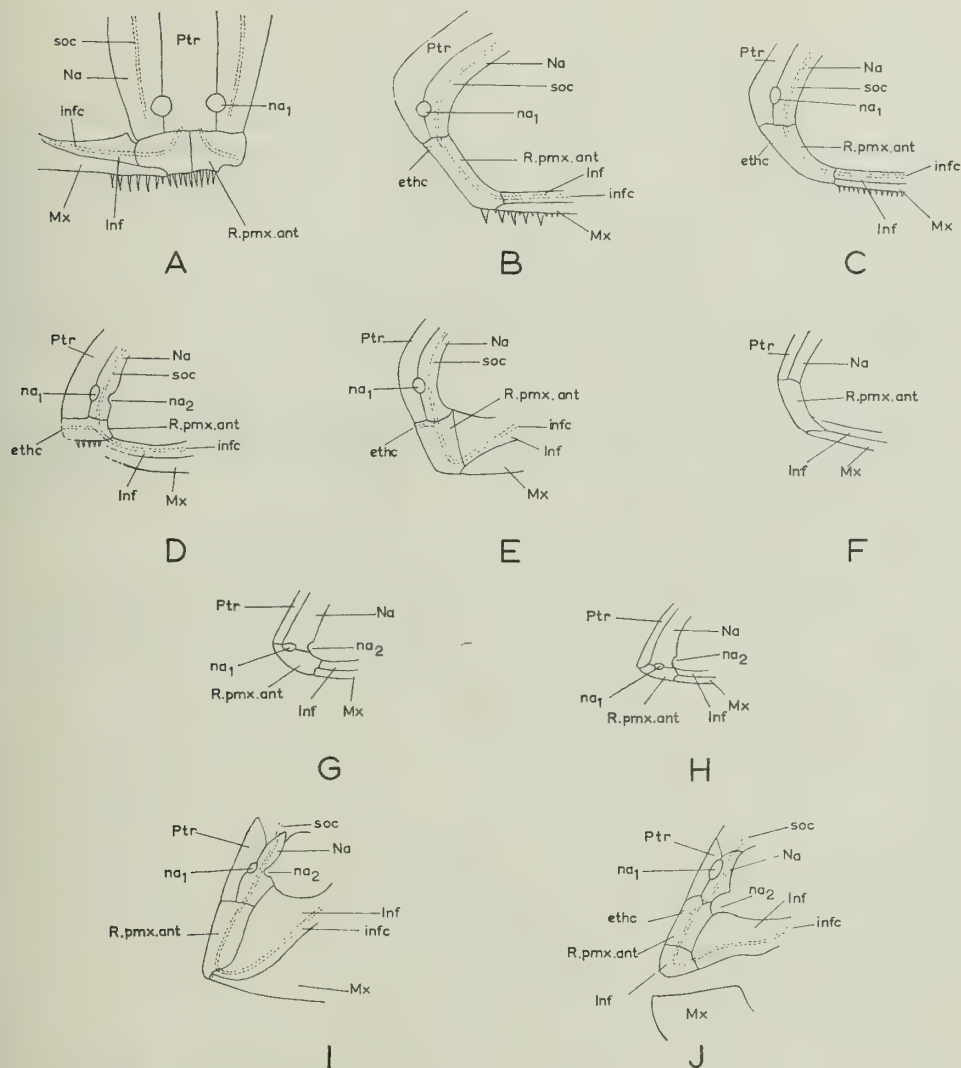


FIG. 16. A. *Canobius elegantulus* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. B. *Rhadinichthys canobiensis* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. C. *Palaeoniscus freislebeni* Blainville. Upper Permian. After Westoll in Aldinger, 1937. D. *Kentuckia deani* (Eastman). Lower Carboniferous. After Rayner, 1951. E. *Paramesolepis tuberculata* (Traquair). Lower Carboniferous. After Moy-Thomas & Dyne, 1938. F. *Diaphorognathus gillioti* (Priem). Lower Triassic. After Brough, 1933. G. *Pyritocephalus sculptus* Fritsch. Upper Carboniferous. After Westoll, 1944. H. *Haplolepis tuberculata* (Newberry). Upper Carboniferous. After Westoll, 1944. I. *Platysomus superbus* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. J. *Bobasatrania mahavavica* White. Lower Triassic. After Lehman, 1957.



boundary of the anterior nostril ( $na_1$ ). The two paired bones of the primitive actinopterygian snout as already mentioned are the nasals and the rostro-premaxillo-antorbital respectively.

The two nasals primitively lie one on either side of the postrostral and are sensory canal bearing elements. The anterior portion of the supraorbital sensory canal passes completely along their length. Most authors use the term nasal when referring to this pair of bones, and since they are intimately associated with the nostrils the terminology is sound and should not give rise to any confusion. Each nasal primitively bears two distinct notches, one for the anterior (in the anterior margin) and the other for the posterior (in the posterior margin) nostril. In subsequent evolution the position of these nostrils alters and one or both of these notches may be lost.

The two rostro-premaxillo-antorbitals lie anterior to the postrostral and nasals and meet in the midline (Text-fig. 16A). The rostro-premaxillo-antorbital primitively contains a three branched part of the infraorbital canal. The infraorbital canal passes forwards from the first infraorbital into the posterior part of the rostro-premaxillo-antorbital. This canal continues from its point of entry to the centre of the bone where it divides into two branches, one of which runs nearly parallel with the postero-dorsal margin and anastomoses with the anterior end of the supraorbital canal at the point where the nasal bone meets the rostro-premaxillo-antorbital. The other of the two branches into which the infraorbital canal divides extends forward as the ethmoid commissure. Thus the sensory canal system in this bone often looks "Y" shaped (Text-fig. 16B, C, D, E, J). I have used the rather cumbersome term rostro-premaxillo-antorbital since by subsequent fragmentation this bone gives rise to the rostral, the antorbital and the premaxilla. For the same bone Moy-Thomas & Dyne (1938) and Rayner (1951) have used the term rostral, while Westoll (1944) has used both dentigerous rostral and pre-maxilla. Nielsen (1942), however, has used a very similar terminology to mine, calling the bone rostro-antorbital-premaxillary. I feel justified in using the term rostro-premaxillo-antorbital rather than Nielsen's (1942) term because by far the most common initial fragmentation of this bone is into two separate bones, the rostro-premaxillary and the antorbital (Text-fig. 18).

The rostro-premaxillo-antorbital primitively bears teeth along its ventral edge as can be seen in *Stegotrachelus finlayi* (Text-fig. 12) and *Cheirolepis trilli* (Text-fig. 14) from the Devonian and in *Canobius elegantulus* (Text-fig. 16A), *Rhadinichthys canobiensis* (Text-fig. 16B) and *Kentuckia deani* (Text-fig. 16D), all from the Lower Carboniferous. Let us now examine the fate of the rostro-premaxillo-antorbital. Fragmentation of this bone has occurred independently in different groups of palaeoniscoids to give at least three different bone patterns. By far the most common pattern was for the rostro-premaxillo-antorbital first to fragment into two separate bones, the rostro-premaxillary and the antorbital. One of the earliest palaeoniscoids to show this fragmentation is *Moythomasia nitida* (Text-fig. 18G) from the Devonian, whilst several of the Lower Carboniferous forms I have described in this paper show a similar pattern (*Cosmoptychius striatus* (Text-fig. 18C), *Watsonichthys pectinatus*



(Text-fig. 18D), *Nematoptychius greenocki* (Text-fig. 18F)). This pattern is still retained in much later forms such as *Lawnia taylorensis* (Text-fig. 18H) from the Permian and *Pteronisculus arambourgi* (Text-fig. 18A) and *Birgeria groenlandica* (Text-fig. 18B) from the Lower Triassic. The rostro-premaxillary in all these examples bears teeth and contains the ethmoid commissure, while the antorbital which lies posterior to it still retains the characteristic "Y" shaped division of the infraorbital sensory canal system. In the antorbital the anteriorly directed branch of the infraorbital canal extends forwards passing through the rostral process and then into the rostro-premaxillary as the ethmoid commissure (see p. 280). The antorbital may or may not bear teeth ventrally, depending upon where the fragmentation occurred. Thus the antorbital bears teeth in such forms as *Cosmoptychius striatus* (Text-fig. 18C), *Watsonichthys pectinatus* (Text-fig. 18D) and *Mesonichthys aitkeni* (Text-fig. 18E), while teeth are not present on the antorbital of *Pteronisculus arambourgi* (Text-fig. 18A), *Birgeria groenlandica* (Text-fig. 18B), *Nematoptychius greenocki* (Text-fig. 18F), *Moythomasia nitida* (Text-fig. 18G) and *Lawnia taylorensis* (Text-fig. 18H).

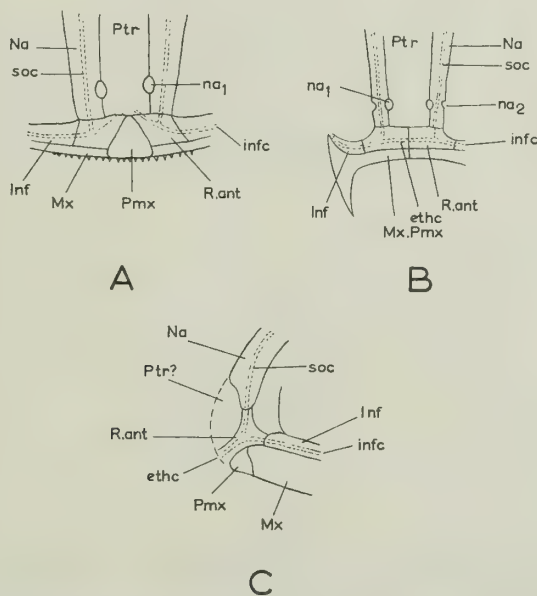


FIG. 17. A. *Canobius ramsayi* Traquair. Lower Carboniferous. After Moy-Thomas & Dyne, 1938. B. *Cornuboniscus budensis* White. Upper Carboniferous. After White, 1939. C. *Cleithrolepis granulata* Egerton. Triassic. After Wade, 1935.

Different but much more uncommon methods of fragmentation of the rostro-premaxillo-antorbital are shown in Text-fig. 17. In *Canobius ramsayi* (Text-fig. 17A), for example, a large central element is present, the toothed premaxilla, while the remainder of the bone from which it fragmented represents the rostro-antorbital and contains the ethmoid commissure. It seems likely that in this case



after the initial fragmentation the two premaxillae have fused to give this single median structure. In *Cleithrolepis granulata* (Text-fig. 17C), fragmentation has resulted in paired premaxillae and a rostro-antorbital again with the contained ethmoid commissure. The condition seen in *Cornuboniscus budensis* (Text-fig. 17B) is more difficult to explain, there being two possible alternatives, either the rostro-premaxillo-antorbital has split into a rostro-antorbital and a paired premaxilla with the latter fusing with the anterior ends of the maxillae of either side, which is the view I favour, or the rostro-premaxillo-antorbital has not fragmented and has thus retained its ancestral condition with the maxillae of either side extending anteriorly to meet in the midline beneath it.

Returning to the more common type of fragmentation—that of the rostro-premaxillo-antorbital into rostro-premaxillary and antorbital, it would seem that this is the ancestral condition from which the later holosteans and teleosts were derived. Going one step further, it appears more likely that the holostean condition was derived from forms which possessed a rostro-premaxillary and a toothless antorbital (i.e. those forms where the antorbital does not take part in the upper jaw margin, viz. *Pteronisculus arambourgi* (Text-fig. 18A), *Birgeria groenlandica* (Text-fig. 18B), *Lawnia taylorensis* (Text-fig. 18H), *Nematoptychius greenocki* (Text-fig. 18F), *Moythomasia nitida* (Text-fig. 18G)) rather than from those forms in which the antorbital bears teeth (i.e. those forms where the antorbital takes part in the formation of the upper jaw margin, viz. *Cosmoptychius striatus* (Text-fig. 18C), *Watsonichthys pectinatus* (Text-fig. 18D), *Mesonichthys aitkeni* (Text-fig. 18E)).

From forms possessing a paired toothed rostro-premaxillary and an antorbital which does not enter into the formation of the upper jaw margin the next step is for the rostro-premaxillary to fragment to give a separate rostral, containing the ethmoid commissure, and a toothed premaxilla (this is in fact the holostean condition, see Text-fig. 19). In *Watsonulus eugnathoides* (Lower Triassic) Text-fig. 19A, this step has not yet occurred and thus in the snout there is still a rostro-premaxillary and an antorbital present, but in other members of the same family, also from the Lower Triassic, fragmentation of the rostro-premaxillary has taken place giving a separate rostral and a premaxilla, the rostral containing the ethmoid commissure (viz. *Parasemionotus labordei* (Text-fig. 19B)). Thus in the pholidophoroid-teleost line this final fragmentation into a separate premaxilla and rostral did not occur until the Lower Triassic (if one believes that the parasemionotids were ancestral to the pholidophoroids, Gardiner, 1960), and similarly in the amioid line (Text-fig. 19G, H, I) since the amioids were undoubtedly also derived from the parasemionotids. In the separate semionotoid line, however, fragmentation of the rostro-premaxillary into rostral and premaxilla had occurred by the Upper Permian as shown by *Acentrophorus varians* (Text-fig. 19J).

At about the same time as this final fragmentation into rostral and premaxilla was taking place the median postrostral bone underwent reduction and was finally lost. The postrostral is not present in the parasemionotids or in the two lines which lead from them, the pholidophoroids and the amioids; it was presumably reduced and lost prior to the parasemionotid grade of organization. However,



the postrostral is still present in the early members of the semionotid line, viz. *Acentrophorus varians* (Text-fig. 19J), *Semionotus capensis* (Gardiner, 1960, text-fig. 71). Correlated with the loss of the postrostral are fundamental changes in the position of the nostrils, which will be dealt with later in the discussion.

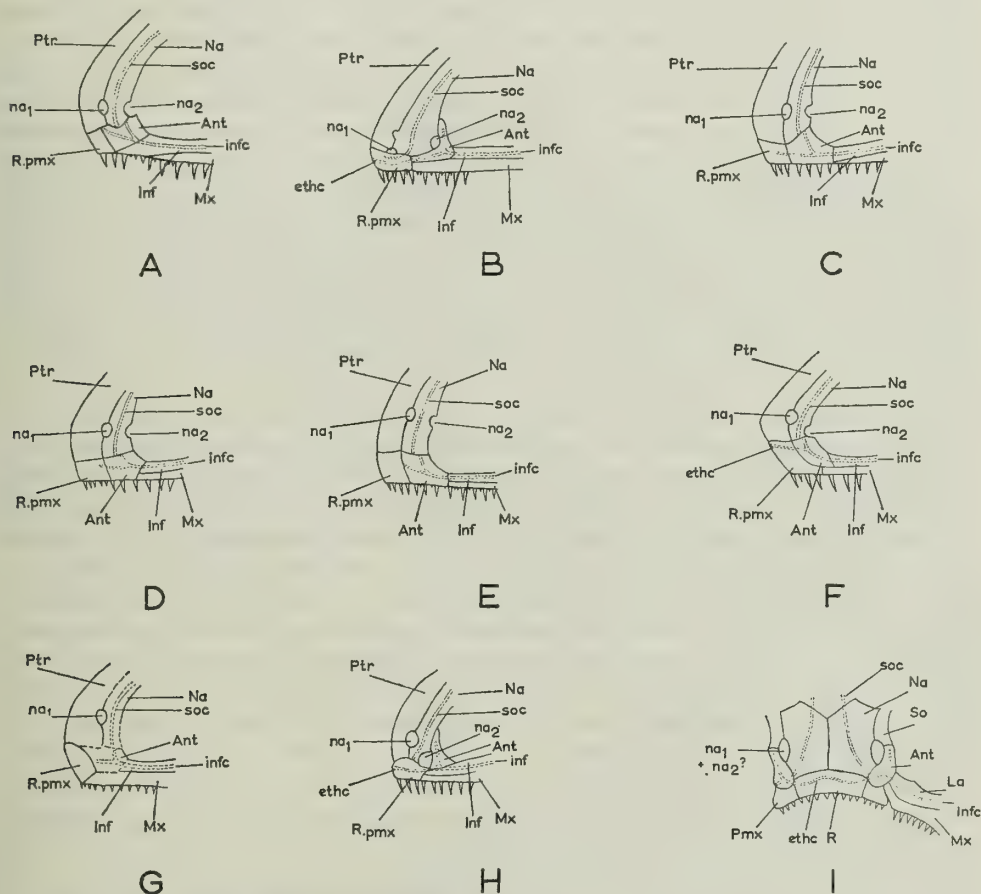


FIG. 18. A. *Pteronisculus arambourgi* Lehman. Lower Triassic. After Lehman, 1952. B. *Birgeria groenlandica* Stensiö. Lower Triassic. After Nielsen, 1949. C. *Cosmoptychius striatus* (Agassiz). Lower Carboniferous. D. *Watsonichthys pectinatus* (Traquair). Lower Carboniferous. E. *Mesonichthys aitheni* n. gen. (Traquair). Upper Carboniferous. F. *Nematoptychius greenocki* (Traquair). Lower Carboniferous. G. *Moythomasia nitida* Gross. Upper Devonian. After Gross, 1955. H. *Lawnia taylorensis* Wilson. Permian. After Wilson, 1953. I. *Ichthyokentema purbeckensis* (Davis). Upper Jurassic. After Griffith & Patterson, 1963.

Summing up, then, as a result of this fragmentation of the palaeoniscoid rostro-premaxillo-antorbital and the reduction and subsequent loss of the postrostral, the snout region of the holostean composed of basically four pairs of bones, the nasals,



rostrals, premaxillae and antorbitals was derived. However, in almost all holosteans and teleosts the rostral is a single bone in the adult condition. Nevertheless, Pehrson (1940) is of the opinion that in *Amia* this single bone represents the numerous separate rostral bones of primitive forms. In *Lepisosteus* the rostral arises as a paired bone in relation to the ethmoid commissure (De Beer, 1937 : 114). Thus it would seem that the rostral was originally paired, as indeed it must have been if we postulate its derivation from the paired rostro-premaxillo-antorbital of primitive forms. That some fusion of the original paired bones of the snout has occurred can be seen in *Birgeria groenlandica* Stensiö from the Lower Triassic where the rostro-premaxilla is a single median bone (formed by the fusion of the originally paired rostro-premaxillaries). Further, in some of the parasemionotids this would also appear to be the case. From such a median single rostro-premaxillary in a parasemionotid the condition described by Griffith and Patterson (1963) in the pholidophoroid *Ichthyokentema purbeckensis* (Davis) (Text-fig. 18I) from the Upper Jurassic could have been derived by the splitting off of two premaxillae to leave a median toothed rostral (for further discussion on this point see Griffith and Patterson, 1963).

Let us now follow the fate of these bones in the teleosts. The nasals are not easily confused, lying as they do anterior to the frontals and always containing the anterior portion of the supraorbital sensory canal. The nasals do, however, show considerable reduction in some groups. The rostral bone only persists as a recognisable bone in a few primitive teleosts ; thus in the Recent *Elops saurus* it is represented by four small components through which the ethmoid commissure runs (Text-fig. 19D). In *Ctenothrissa* from the Cenomanian (Text-fig. 19E), a fish which in grade of organization stands between the Elopidae and the more advanced acanthopterygians (Patterson, 1963), the rostral (dermethmoid of many authors) is a small plate of dermal bone intimately associated with the underlying mesethmoid, and the ethmoid commissure no longer passes through this bone but must have run above it. The rostral is finally unrecognizable in the more advanced acanthopterygians and in other advanced teleosts.

The premaxilla, which is still small in *Pholidophorus* from the Triassic, becomes much enlarged in the later teleosts, while the antorbital becomes reduced and lost. The antorbital is still present in some primitive teleosts such as *Elops saurus* (Text-fig. 19D) and see Gosline (1961 : 22) for a few others, while Patterson (1963) has given a good evolutionary series showing its reduction and loss within the acanthopterygians. *Ctenothrissa radians* (Text-fig. 19E) from the Cenomanian still retains a moderate-sized antorbital but in *Hoplopteryx sinus*, again from the Cenomanian and a member of the Trachichthyidae, it is represented by a very small element (the infraorbital sensory canal no longer piercing it even) and this is the last appearance of the antorbital in the acanthopterygians. However, some Recent members of the family Holocentridae, which is a family close to the Trachichthyidae, still possess an antorbital. At the same time that the antorbital was being reduced there was an increase in size of the first infraorbital in the teleosts. The first infraorbital (the most anterior infraorbital) is that bone which in the primitive palaeoniscoid

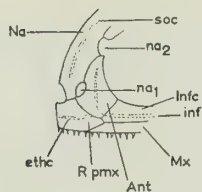


lies immediately behind the rostro-premaxillo-antorbital, above the maxilla and through which the infraorbital canal passes. In the teleost this same bone is normally referred to as the lachrymal. I would favour the retention of this dual nomenclature, calling this bone the first infraorbital in anything below the teleost grade of organization, and lachrymal in the teleost. Since the antorbital is usually wanting in teleosts it would be as well to define the exact position of the lachrymal. In teleosts and pholidophoroids the lachrymal always articulates with the edge of the lateral ethmoid, its ventral edge lies lateral to the maxilla but not necessarily touching it, and the palatine articulates with its inner surface.

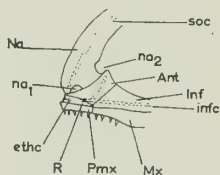
Having examined the homologies of the different bones that go to make up the actinopterygian snout, the more difficult problem of the position of the nostrils may be examined. No one, apart from Saint-Seine (1949 : 292), appears to have discussed or even mentioned this basic and important question. The primitive palaeoniscoid ancestors possessed two pairs of nostrils, the anterior nostril ( $na_1$ ) lying between the postrostral and the anterior edge of the nasal, and the posterior nostril ( $na_2$ ) lying in the posterior edge of the nasal, these two nostrils then being separated by the nasal bone and with the contained branch of the supraorbital sensory canal passing between them (Text-fig. 16D, I, J ; see also Recent *Acipenser* Text-fig. 20A). It seems probable that in many of the reconstructions (Text-fig. 16A, B, C, E, F) the rather more insignificant posterior nostril has been omitted by the different authors, since it is often only represented by the smallest of notches. In all these primitive palaeoniscoids (Text-fig. 16) the infraorbital canal anastomoses with the supraorbital sensory canal at the junction between the nasal and the rostro-premaxillo-antorbital. With the initial fragmentation of the rostro-premaxillo-antorbital into rostro-premaxillary and antorbital this anastomosis between the infraorbital and supraorbital sensory canal is broken, the dorsally directed branch of the infraorbital canal in the antorbital reaching the dorsal margin of the antorbital posteriorly to the point where the supraorbital canal reaches the ventral margin of the nasal (Text-fig. 18). In subsequent evolution towards the holostean-teleost condition the shape of the antorbital has changed, it has become produced dorsally until that portion containing the dorsal extension of the infraorbital sensory canal has come to lie posterior to the nasal and at the same time to form the posterior margin of the posterior nostril (Text-figs. 18B, H ; 19C, D, I).

In order to arrive at the condition seen in both holosteans and teleosts, with regard to the nostrils, it is necessary to get both of the nostrils to the lateral side of the supraorbital sensory canal. The problem is not an easy one and to postulate the migration of the anterior nostril appears to me to be the only solution. There are certain palaeoniscoids which show how this migration may have occurred. For example, in *Birgeria groenlandica* (Text-fig. 20B), the anterior nostril ( $na_1$ ) lies right at the antero-ventral extremity of the nasal bone. Again, in *Haplolepis tuberculata* (Text-fig. 20C) the anterior nostril lies midway along the ventral edge of the nasal. The real difficulty would seem to be for the anterior nostril to cross the supraorbital sensory canal, however the anastomosis between the supraorbital and infraorbital sensory canals has been broken, so that migration of the anterior

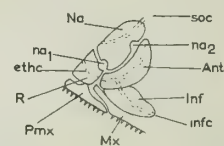




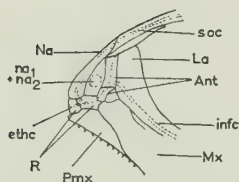
A



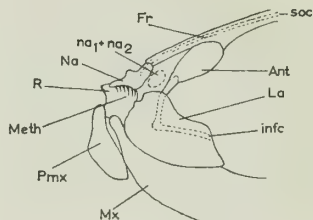
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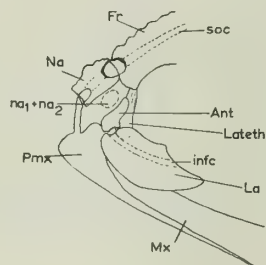
C



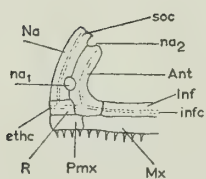
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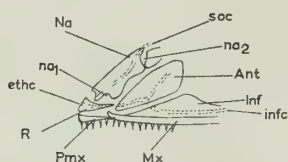
E



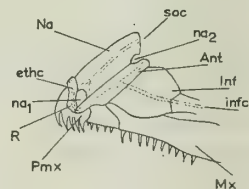
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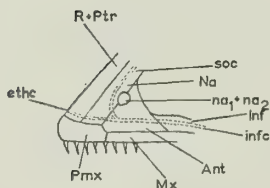
G



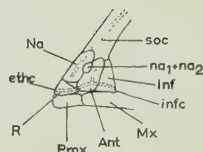
H



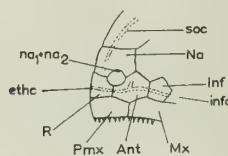
I



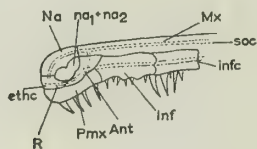
J



K



L



M



nostril down and round the ventral limits of the nasal is now possible. A further clue to this complex problem is given by a study of the Recent *Polypterus senegalus* (Text-fig. 20D) in which the anterior nostril is confluent with the posterior nostril, with the anterior portion of the nasal bone and its contained supraorbital sensory canal partially separating them. It would seem that in *Polypterus senegalus* we have the answer to the problem, that is that the anterior nostril migrated round the anterior edge of the nasal, passing round the contained supraorbital sensory canal to end up on the posterior side of the nasal. The migration of the anterior nostril can be correlated with the reduction and subsequent loss of the postrostral, which primitively formed the anterior boundary of this nostril.

Let us now examine some of the later actinopterygians to trace the subsequent fate of this anterior nostril. In the Parasemionotidae the anterior nostril has already migrated to the lateral nasal margin, so that the nasal now has two separate notches in its lateral border for the anterior and posterior nostrils respectively (Text-fig. 19A, B). In the more advanced Pholidophoridae (Text-fig. 19C) the two nostrils are still quite separate but in the later teleosts further upward migration of the anterior nostril has taken place until both the anterior and posterior nostrils have become confluent and the teleost condition is one in which normally only one nostril (however still clearly divided internally) is to be seen.

In the Amioidea, which were derived from the same ancestral stock as the Pholidophoroidea (Gardiner, 1960) both nostrils are present, both lying lateral to the supraorbital sensory canal (Text-fig. 19G, H, I).

In the Semionotoidea, however, only one nostril is present (Text-fig. 19J, K, L, M), and this single aperture represents the fusion of the anterior with the posterior nostril<sup>1</sup>. Already in the Permian *Acentrophorus* (Text-fig. 19J), this fusion had occurred and this lends further weight to the argument that the Semionotoidea and Amioidea had quite separate ancestries (Gardiner, 1960).

Unfortunately the condition of the nostrils in the Pycnodontoidea is not at all clear, but in both the Platysomidae (Text-fig. 16I) and the Amphicentridae (and from one or other of these two groups the pycnodonts must have been derived), and also the later Bobasatraniaidae (Text-fig. 16J), the snout is of the primitive palaeoniscoid condition with the nostrils still one on either side of the supraorbital sensory canal.

In the Aspidorhynchoidea the condition is similar to that in the teleosts in that the two nostrils have become confluent.

FIG. 19. A. *Watsonulus eugnathoides* Piveteau. Lower Triassic. After Lehman, 1952. B. *Parasemionotus labordei* Lehman. Lower Triassic. After Lehman, 1952. C. *Pholidophorus similis* Woodward. Kimeridgian. After Saint-Seine, 1949. D. *Elopsaurus* Linnaeus. Recent. E. *Ctenothrissa radians* (Agassiz). Cenomanian. After Patterson, 1963. F. *Hoplopteryx sinus* Woodward. Cenomanian-Turonian. After Patterson, 1963. G. *Paracentrophorus madagascariensis* Piveteau. Lower Triassic. After Gardiner, 1960. H. *Caturus drieri* Thiollère. Kimeridgian. After Saint-Seine, 1949. I. *Amia calva* Linnaeus. Recent. J. *Acentrophorus varians* (Kirkby). Upper Permian. After Gardiner, 1960. K. *Lepidotes semiserratus* Agassiz. Upper Lias. L. *Dapedium politum* Leach. Lower Lias. M. *Lepisosteus osseus* Linnaeus. Recent.

<sup>1</sup> In some specimens of *Lepisosteus* the two nostrils may be separated by a narrow bridge of bone.



Finally, anastomosis of the infraorbital sensory canal with the supraorbital canal can take place at a later stage if the two components lie close enough together. This has occurred in the Recent *Polypterus senegalus* (Text-fig. 20D) and in the Recent *Lepisosteus osseus* (Text-fig. 19M), while a similar condition is observable in *Paracentrophorus madagascariensis* (Text-fig. 19G) from the Lower Triassic.

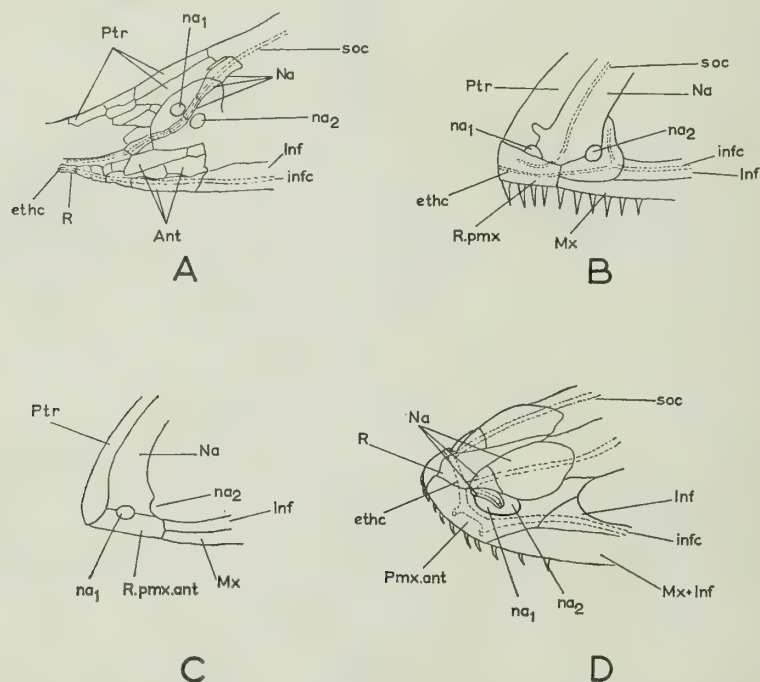


FIG. 20. A. *Acipenser sturio* Linnaeus. Recent. B. *Birgeria groenlandica* Stensiö. Lower Triassic. After Nielsen, 1949. C. *Haplilepis tuberculata* (Newberry). Upper Carboniferous. After Westoll, 1944. D. *Polypterus senegalus* Cuvier. Recent. Partly after Jarvik, 1942.

#### IV. SUMMARY

This paper is intended as a clearing of the ground for a revision of the palaeoniscoid fauna of the British Carboniferous. The type species of four genera from this fauna are redescribed, and for comparative purposes members of four Devonian and two Permian genera are redescribed.

Three new palaeonisciform families are erected. They are the Cosmoptychiidae, closely allied to the Acrolepidae of Aldinger (1937); the Rhabdolepidae, a family fairly close to the Elonichthyidae of Aldinger (1937), and the Stegotrachelidae. The family Tegeolepidae is shown to be intermediate in structure between the Palaeonisciformes and the Chondrosteiformes. A new genus *Mesonichthys* is erected for *Elonichthys aitkeni* Traquair (1886), and a new species, *R. saarbrueckensis*, is added to the genus *Rhabdolepis* Troschel (1857).



The homologies of the bones of the actinopterygian snout are discussed, and it is shown that the primitive actinopterygian snout was composed of three bones only, the paired nasals, the paired rostro-premaxillary-antorbital and the median postrostral. Subsequent fragmentation of the rostro-premaxillary-antorbital has occurred independently in different groups of palaeoniscoids to give at least three different bone patterns. The most common pattern was for the rostro-premaxillary-antorbital to split into two bones, the rostro-premaxillary and the antorbital, and this type of snout appears to have been present in the ancestors of the holosteans and teleosts. Changes in the position of the nostrils during actinopterygian evolution are also discussed, and it is suggested that the condition in teleosts has been reached by migration of the anterior nostril round the ventral edge of the nasal, this migration following breakage of the anastomosis between the infra- and supra-orbital sensory canals, and being correlated with loss of the postrostral.

#### V. ACKNOWLEDGMENTS

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## VII. LETTERING USED IN TEXT-FIGURES

|            |                                          |                 |                                    |
|------------|------------------------------------------|-----------------|------------------------------------|
| A          | anal fin                                 | l               | lepidotrichia                      |
| Ang        | angular                                  | La              | lacrimal                           |
| Ant        | antorbital                               | Lateth          | lateral ethmoid                    |
| a.Op       | accessory opercular                      |                 |                                    |
| ap         | anterior pit line                        | mc              | mandibular sensory canal           |
| Ax         | axonost                                  | Meth            | mesethmoid                         |
|            |                                          | mp              | median pit line                    |
| Bd         | basidorsal                               | Mx              | maxilla                            |
| Bo         | baseost                                  |                 |                                    |
| Br         | branchiostegal ray                       | Na              | nasal                              |
| Bv         | basiventral                              | na <sub>1</sub> | anterior nasal aperture (nostril)  |
|            |                                          | na <sub>2</sub> | posterior nasal aperture (nostril) |
| Cl         | cleithrum                                | Op              | opercular                          |
| Clav       | clavicle                                 | or              | orbit                              |
| D          | dorsal fin                               | orp             | postmaxillary sensory line         |
| Den        | dentary                                  |                 |                                    |
| Dpt        | dermopterotic                            | Pa              | parietal                           |
| dr         | distal radials                           | Pcl             | postcleithrum                      |
| Dsp        | dermosphenotic                           | pi              | pineal foramen                     |
| Dsp.Inf.so | dermosphenotic-infraorbital-supraorbital | Pmx             | premaxilla                         |
| Dyh        | dermohyal                                | Pmx.ant         | premaxillo-antorbital              |
|            |                                          | Pop             | preopercular                       |
| ethc       | ethmoid commissure                       | pp              | posterior pit line                 |
| Exsc       | extrascapular                            | Ptr             | postrostral                        |
|            |                                          | Pv              | pelvic plate                       |
| Fr         | frontal                                  | R               | rostral                            |
|            |                                          | r               | radial                             |
| Gu         | gular plate                              | R.ant           | rostrom-antorbital                 |
|            |                                          | r.p             | rostral process                    |
| ha         | haemal arch                              | R.pmx           | rostrom-premaxillary               |
| hc         | supramaxillary sensory line              | R.pmx.ant       | rostrom-premaxillo-antorbital      |
| Hm         | hyomandibular                            |                 |                                    |
| Hy         | hypural                                  | Sbo             | suborbital                         |
| Ih         | infrahaemal                              | ScCor           | scapulo-coracoid                   |
| Inf        | infraorbital                             | Scl             | supracleithrum                     |
| infc       | infraorbital sensory canal               | s.com           | supratemporal commissure           |
| Inf.so     | infraorbital-supraorbital                | sc.r            | sclerotic ring                     |
| Iop        | interopercular                           | Sn              | supraneural                        |
| Iv         | interventral                             | So              | supraorbital                       |
|            |                                          | soc             | supraorbital sensory canal         |



|          |                                                 |          |                                             |
|----------|-------------------------------------------------|----------|---------------------------------------------|
| Sop      | subopercular                                    | B.M.N.H. | British Museum (Natural                     |
| sps      | spiracular notch                                |          | History), London                            |
| Scs      | suprascapular                                   | R.S.M.   | The Royal Scottish Museum,<br>Edinburgh     |
| A.M.N.H. | American Museum of Natural<br>History, New York | U.M.Z.C. | University Museum of Zoology,<br>Cambridge. |



PLATE I

*Tegeolepis clarki* (Newberry)

Underside of fish, showing pectoral fins. B.M.N.H., P.9402.  $\times \frac{3}{8}$ .



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Pv

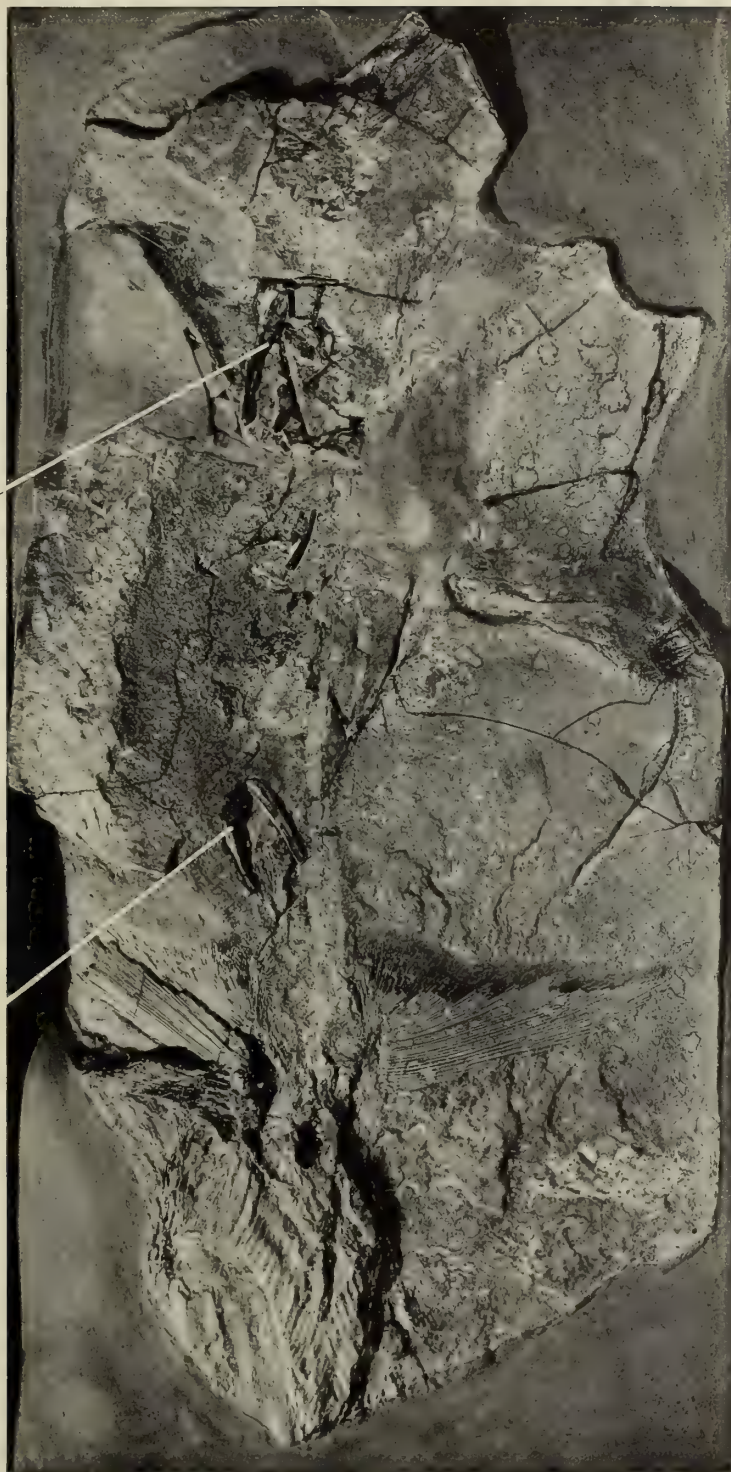












PLATE 2

*Tegeolepis clarki* (Newberry)

Upper and Lower jaw. B.M.N.H., P.45312.  $\times \frac{3}{4}$ .















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FAUNAS OF THE BALA DISTRICT,  
MERIONETHSHIRE

A. WILLIAMS

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY

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# THE CARADOCIAN BRACHIOPOD FAUNAS OF THE BALA DISTRICT, MERIONETHSHIRE



BY

ALWYN WILLIAMS, Ph.D.

(Professor of Geology, The Queen's University, Belfast)

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By A. WILLIAMS

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## SYNOPSIS

A study of the Caradocian brachiopods of the Bala district has shown that the majority are at least specifically distinct from their Shropshire contemporaries. Consequently the correlation between the rocks of North Wales and the Welsh Borderlands proved to be less certain than was anticipated. The differences appear to be accentuated by the existence of three distinct assemblages—the *Nicolella*, *Dinorthis* and *Howellites* associations—within the Caradocian



successions at Bala. Each association seems to have enjoyed its own optimum sedimentary environment which was rarely sufficiently widespread to enable species to flourish simultaneously in both regions. Detailed systematic analyses that led to this interpretation, are presented and involve the description of fifty-one species and subspecies, of which seventeen are new, belonging to thirty-five genera including the new ones—*Paracraniops*, *Rhactorthis* and *Crem-northis*, and two new families are introduced.

#### I. INTRODUCTION AND ACKNOWLEDGMENTS

THE shelly facies of the Bala district, Merionethshire, have played a part in the synthesis of Lower Palaeozoic Stratigraphy that is out of all proportion to their intrinsic worth because, having been described by Sedgwick (1845 : 7) as an important subdivision of his Cambrian System, they became the touchstone for both him (Sedgwick & M'Coy 1855 : xx) and Murchison (1854 : 7, 8) in furthering the merits of their respective systemic classifications. The ambiguity arising from this dual function survived even the objective pen of Lapworth who in his definition of the Ordovician system (Lapworth 1879) continued to use the "Bala Group" although, as he commented, the faunas were not as well known as those from Murchison's "Caradoc Formation". This statement may seem surprising in face of the researches on Bala fossils conducted by such palaeontologists as M'Coy (1851 ; 1852), Salter and J. de C. Sowerby (see Sedgwick 1845 : 20) but the fact remains that their publications were mainly descriptive catalogues of collections recovered by a geologist who had already decided what the stratigraphical arrangement was. Actually, apart from certain aspects of Ruddy's studies (1897), it was not until 1922, when the late Dr. G. L. Elles published an account of the rocks to the south-east of Bala Lake, that field relationships and palaeontology were used concurrently to determine the faunal succession. One of the most important features of her work was the reiteration of Sedgwick's belief that the differences between the Upper and Lower Bala faunas, as typified by fossils from the Rhiwlas and "Bala" Limestones respectively, did not reflect so much a break as a change in emphasis (Elles 1922 : 164). This conclusion however was challenged by Bancroft (1928) in a brief but important paper which was the forerunner of some convincing demonstrations (1933 ; 1945) that shelly faunas can be used for detailed correlation of the Lower Palaeozoic rocks and that by doing so the succession at Bala can be shown to include only about one-half of the Caradocian of the Welsh Borderland and only the upper part of the Ashgillian of the Lake District.

By 1952 reconnaissance work had shown that there were discrepancies not only in Elles' map but also in the correlations afforded by Bancroft's recorded traverses. Since neither of them had examined the rocks to the north-east of the Lake, Dr. D. A. Bassett, Prof. H. B. Whittington and I decided to revise the stratigraphy of the entire district and at the same time to obtain large fossil collections with a view to re-examining the brachiopods and the trilobites, the principal elements of the Bala faunas. The aims of this joint undertaking have now been completed. The stratigraphical account, under triple authorship, together with a structural analysis by Dr. Bassett are being submitted to the Geological Society of London ; while the systematic revision of the trilobites conducted by Prof. Whittington, is being published by the Palaeontographical Society. These studies, including the one



presented below, are so dependent on one another and so completely complementary that no attempt has been made here either to enumerate entire fossil faunas or to give a stratigraphical account other than the outline required to illustrate the problems arising from correlations based on brachiopod assemblages: for such details the reader may refer to the papers just mentioned.

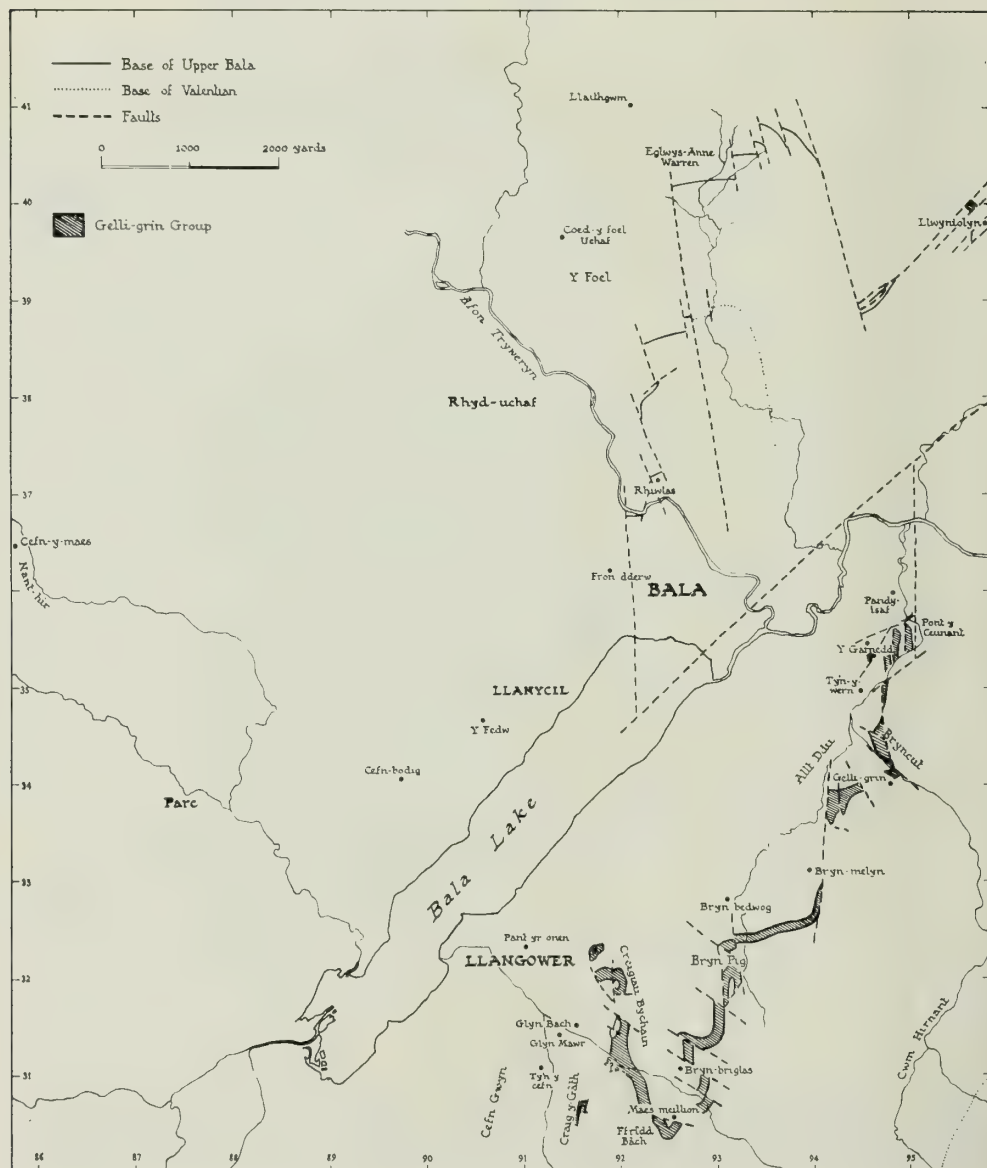


FIG. 1. Sketch map of the Bala District.



In order to be as objective as possible, the variability of brachiopod samples has been treated quantitatively according to the procedures adopted elsewhere (Williams 1962 : 69-79). Much of Bancroft's systematic work is, of course, quantitative in the sense that he used notations to describe the patterns of radial ornamentation in brachiopods or the distribution of pits in trinucleid trilobite brims. But he frequently ignored other morphological changes which are systematically at least as important as those he concentrated on ; and in any event, he never subjected his data to tests of significance so that his taxonomic treatment of samples tended to negate the precision of his methods. Consequently those species of his that may have been relevant to the identification of the Bala brachiopods have been re-investigated as critically as those proposed during the last century. Such comparative studies of samples from the Welsh Borderland and elsewhere have naturally provided a great deal of information and when the new data have led to a revision of our concept of an established species or to a more precise idea of its variability, an emended description of that species, even if it has not been found in the Bala district, has been included.

A host of friends from as far apart as Pasadena, Lund and Edinburgh have visited my colleagues and me during our field work and for pertinent observations here and recovered fossils there we express our appreciation in full confidence that they will not mind remaining anonymous. Special mention however, must be made of Mrs. Dorothy Whittington for her efficient taxi-service and her indefatigable collecting : without such aid we would have been working in the district yet. The brachiopod study itself has been greatly facilitated by access to large collections of topotypic material from the Welsh Borderland made by Mr. A. D. Wright and by the invaluable help in computation and photographic preparation of Miss Helen Lesser, research assistant in the Department of Geology at Queen's University : I am indeed indebted to them for their labours. Finally, it is a pleasure to record that specimens from the British and Sedgwick Museums were readily loaned by Dr. W. T. Dean and Mr. A. G. Brighton and that grants towards the cost of field work over these last ten years have been received from the University of Glasgow and the Queen's University, Belfast.

## II. THE FAUNAL ASSEMBLAGES AND CORRELATION

Sixty-four species and subspecies of brachiopods, belonging to forty-two inarticulate and articulate genera, have been recovered from the Caradocian rocks of the Bala-Arenig district, Merionethshire. The succession consists essentially of about 4,500 ft. of mudstones and siltstones with minor ashes and sandstones and is poorly fossiliferous, except for the Gelli-grŷn Group and parts of the Allt Ddu Group, so that the brachiopods recorded below as typical of the Derfel Limestone (see Whittington & Williams 1955) and the rest of the Nant Hir Group were collected from three and four localities respectively ; even the Glyn Gower list is based on collections from about a dozen exposures of the upper part of that Group. This sporadic occurrence of fossils is accentuated by their restriction mainly to bedding planes separated by variable thicknesses of sediments that have been disturbed by worm burrowings but are otherwise devoid of organic remains. Such bedding



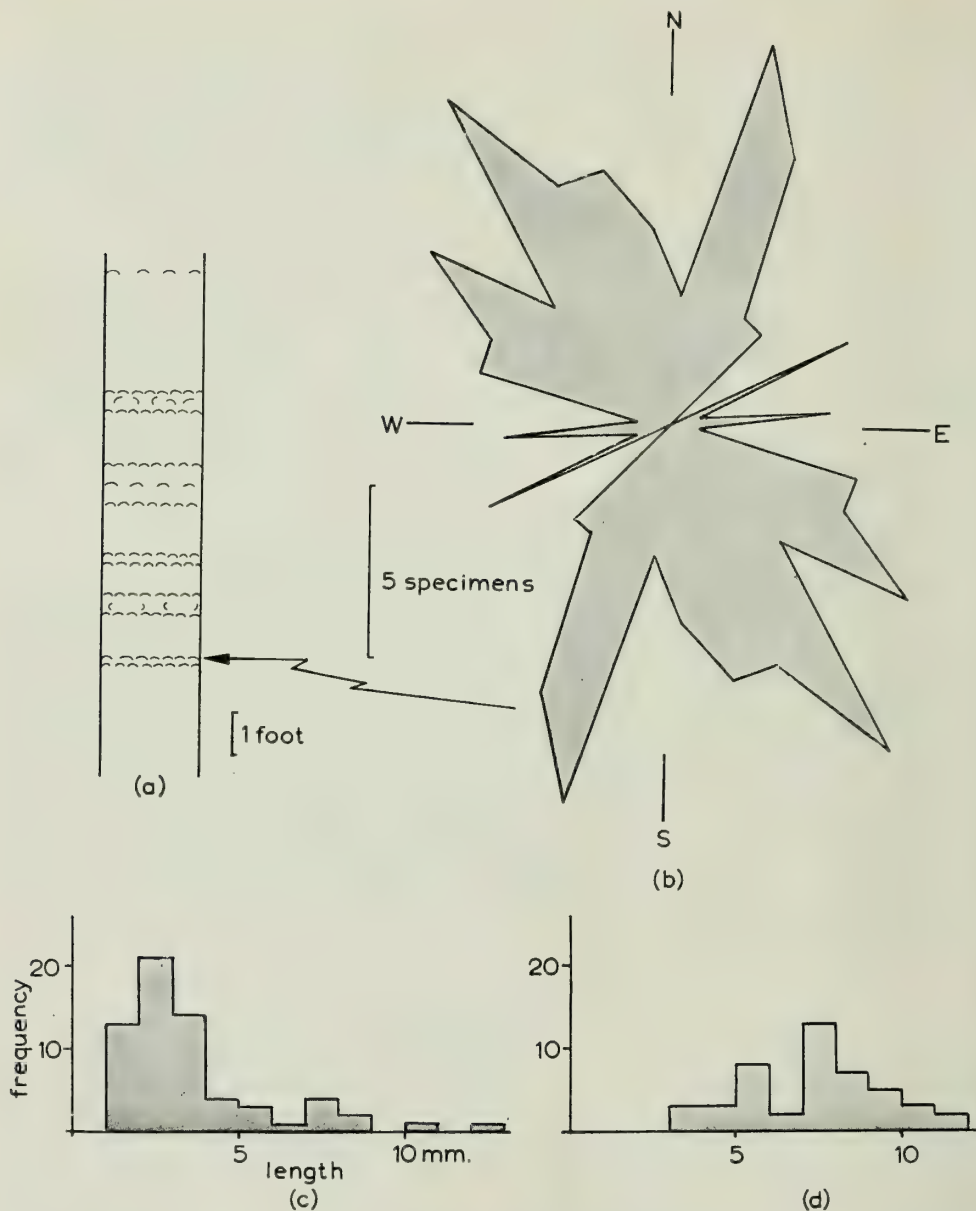


FIG. 2. Some data on the distribution of fossil brachiopods in the Caradocian sediments of Bala : (a) the occurrence of fossils (represented by small arcs) in 12 ft. 7 in. of Lower Allt Ddu siltstones exposed in the southern end of the roadside cutting south-west of Llanycil ; (b) the corrected orientations of the hinge-lines of 106 specimens of *Dinorthis berwynensis* (Whittington), *Heterorthis* cf. *retvorsistria* (M'Coy) and *Reuschella* cf. *horderleyensis* Bancroft taken from one bedding plane in the Lower Allt Ddu siltstones



planes are usually crowded with water-sorted assemblages so that the size-frequency distribution of most species from the coarser sediments tend to be strongly unimodal with a negative skew (Text-fig. 2). Yet, although shells are almost invariably disarticulated, both valves, even when they are quite dissimilar in shape, are well represented in any sample and are rarely broken or abraded. They show also the low degree of preferred orientation that one would associate with the winnowing of a community existing *in situ* rather than the accumulation of drifted remains (Text-fig. 2) ; and the fauna given below has been so interpreted as including the remnants of repeated colonizations of what was mostly an unfavourable environment for permanent occupation.

The distribution of the various species and subspecies is given in the following list in which

- 1, represents the Derfel Limestone at the base of the Nant Hir Group ;
- 2, the rest of the Nant Hir Group (species indicated by asterisks are the only ones recorded above the Cefn-y-maes horizon) ;
- 3, the Glyn Gower Group ;
- 4, the Lower Allt Ddu Group up to and including beds with *Dinorthis berwynensis* (Whittington) and *Heterorthis retrorsistria* (M'Coy) ;
- 5, the Middle Allt Ddu Group ;
- 6, the Upper Allt Ddu Group down to and including beds with *Howellites ultima* Bancroft ;

and 7, the Gelli-grŷn Group.

|                                                                   | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|-------------------------------------------------------------------|---|---|---|---|---|---|---|
| <i>Anisopleurella multiseptata</i> Williams . . . . .             | × | — | — | — | — | — | — |
| <i>Bancroftina</i> sp. . . . .                                    | — | — | — | — | — | — | × |
| <i>Bellimurina incommoda</i> sp. nov. . . . .                     | — | — | — | — | — | — | × |
| <i>Bicuspidina spiriferoides</i> (M'Coy) . . . . .                | — | — | — | × | — | × | × |
| <i>Cremnorthis parva</i> gen. et sp. nov. . . . .                 | — | — | — | — | — | — | × |
| <i>Cyclospira</i> sp. . . . .                                     | — | — | — | — | — | — | × |
| <i>Cyrtonotella</i> aff. <i>kukersiana</i> (Wysogorski) . . . . . | × | — | — | — | — | — | — |
| <i>Dalmanella modica</i> sp. nov. . . . .                         | — | — | — | — | — | — | × |
| <i>Dalmanella</i> sp. . . . .                                     | — | — | × | × | — | — | — |
| <i>Dinorthis berwynensis</i> (Whittington) . . . . .              | — | * | × | × | — | — | — |
| <i>Dinorthis berwynensis angusta</i> subsp. nov. . . . .          | — | — | — | — | — | × | × |
| <i>Dolerorthis duftonensis proluxa</i> subsp. nov. . . . .        | — | — | — | — | — | — | × |
| <i>Dolerorthis tenuicostata</i> Williams . . . . .                | × | — | — | — | — | — | — |
| <i>Dolerorthis</i> sp. . . . .                                    | — | — | — | — | — | × | — |
| <i>Eoplectodonta lenis</i> Williams . . . . .                     | × | — | — | — | — | — | — |
| <i>Eoplectodonta</i> cf. <i>rhombica</i> (M'Coy) . . . . .        | — | — | — | — | — | — | × |
| <i>Glossorthis</i> sp. . . . .                                    | × | — | — | — | — | — | — |
| <i>Glyptomena</i> cf. <i>osloensis</i> (Spjeldnaes) . . . . .     | — | — | — | — | — | — | × |
| <i>Hedstroemina?</i> spp. . . . .                                 | — | × | × | — | — | — | — |

south-west of Llanycil ; (c) the length-frequency distributions of 18 pedicle valves and 46 brachial valves of *Onniella* cf. *soudleyensis* (Bancroft) from the Nant Hir siltstones at Cefn-y-maes and (d) 18 pedicle valves and 28 brachial valves of *O. ostentata* sp. nov. from the Gelli-grŷn Group.



|                                                       |   |   |   |   |    |   |   |   |   |   |
|-------------------------------------------------------|---|---|---|---|----|---|---|---|---|---|
| <i>Heterorthis</i> cf. <i>retrorsistria</i> (M'Coy)   | . | . | . | — | —  | — | x | — | — | — |
| <i>Horderleyella</i> sp.                              | . | . | . | x | —  | — | — | — | — | — |
| <i>Howellites intermedia</i> Bancroft                 | . | . | . | — | —  | — | — | x | — | — |
| <i>Howellites antiquior</i> (M'Coy)                   | . | . | . | — | —  | — | — | — | — | x |
| <i>Howellites striata</i> Bancroft                    | . | . | . | — | —  | — | x | x | — | — |
| <i>Howellites ultima</i> Bancroft                     | . | . | . | — | —  | — | — | — | x | — |
| <i>Howellites</i> sp.                                 | . | . | . | x | —  | — | — | — | — | — |
| <i>Kiaeromena</i> cf. <i>kjerulfi</i> (Holtedahl)     | . | . | . | — | —  | — | — | — | x | — |
| <i>Kiaeromena</i> sp.                                 | . | . | . | x | —  | — | — | — | — | — |
| <i>Kjaerina</i> sp.                                   | . | . | . | x | —  | — | — | — | — | — |
| <i>Kullervo</i> aff. <i>panderi</i> (Öpik)            | . | . | . | x | —  | — | — | — | — | — |
| <i>Leptaena ventricosa</i> sp. nov.                   | . | . | . | — | —  | — | x | — | x | x |
| <i>Leptestiina derfelensis</i> (Jones)                | . | . | . | x | —  | — | — | — | — | — |
| <i>Leptestiina oepiki</i> (Whittington)               | . | . | . | — | —  | — | — | — | — | x |
| <i>Lingulella</i> cf. <i>ovata</i> (M'Coy)            | . | . | . | — | —  | — | x | — | — | x |
| <i>Lingulella</i> cf. <i>tenuigranulata</i> (M'Coy)   | . | . | . | — | —  | — | — | — | — | x |
| <i>Lingulella</i> sp.                                 | . | . | . | — | x  | — | — | — | — | — |
| <i>Macrocœlia prolata</i> sp. nov.                    | . | . | . | — | —  | x | x | x | x | x |
| <i>Nicolella actoniae obesa</i> subsp. nov.           | . | . | . | — | —  | — | — | — | — | x |
| <i>Nicolella humilis</i> Williams                     | . | . | . | x | —  | — | — | — | — | — |
| <i>Onniella</i> aff. <i>avelinei</i> Bancroft         | . | . | . | x | —  | — | — | — | — | — |
| <i>Onniella ostentata</i> sp. nov.                    | . | . | . | — | —  | — | — | — | — | x |
| <i>Onniella</i> cf. <i>soudleyensis</i> (Bancroft)    | . | . | . | — | x  | — | — | — | — | — |
| <i>Orbiculoidea</i> sp.                               | . | . | . | — | —  | — | — | — | — | x |
| <i>Orthambonites cessata</i> sp. nov.                 | . | . | . | — | —  | — | — | — | — | x |
| <i>Oxoplectia mutabilis</i> Williams                  | . | . | . | x | —  | — | — | — | — | — |
| <i>Oxoplectia</i> sp.                                 | . | . | . | — | —  | — | — | — | — | x |
| <i>Palaeostrophomena magnifica</i> Williams           | . | . | . | x | —  | — | — | — | — | — |
| <i>Paracraniops macella</i> gen. et sp. nov.          | . | . | . | — | —  | — | — | — | — | x |
| <i>Platystrophia precedens major</i> Williams         | . | . | . | x | —  | — | — | — | — | — |
| <i>Platystrophia</i> cf. <i>sublimis</i> Öpik         | . | . | . | — | —  | — | — | — | — | x |
| <i>Pseudocrania</i> cf. <i>divaricata</i> M'Coy       | . | . | . | — | —  | — | — | — | — | x |
| <i>Reuschella</i> cf. <i>horderleyensis</i> Bancroft  | . | . | . | — | *  | x | x | x | — | — |
| <i>Reuschella horderleyensis undulata</i> subsp. nov. | . | . | . | — | —  | — | — | — | x | x |
| <i>Rhactorthis crassa</i> gen. et sp. nov.            | . | . | . | — | —  | — | — | — | — | x |
| <i>Rostricellula sparsa</i> sp. nov.                  | . | . | . | — | —  | — | — | x | x | — |
| <i>Salopia salteri gracilis</i> Williams              | . | . | . | x | —  | — | — | — | — | — |
| <i>Salopia</i> sp.                                    | . | . | . | — | —  | — | — | — | — | x |
| <i>Sericoidea abdita</i> Williams                     | . | . | . | x | x  | — | — | — | — | — |
| <i>Sericoidea</i> sp.                                 | . | . | . | — | —  | — | — | — | — | x |
| <i>Skenidioides</i> cf. <i>costatus</i> Cooper        | . | . | . | — | —  | — | — | — | — | x |
| <i>Sowerbyella musculosa</i> sp. nov.                 | . | . | . | — | —  | — | — | — | x | — |
| <i>Sowerbyella sericea permixta</i> subsp. nov.       | . | . | . | — | x* | x | x | x | — | — |
| <i>Sowerbyella</i> sp.                                | . | . | . | x | —  | — | — | — | — | — |
| <i>Strophomena</i> sp.                                | . | . | . | — | —  | — | — | — | x | x |
| <i>Vellamo</i> sp.                                    | . | . | . | — | —  | — | x | — | — | — |

The most important recent contribution to our understanding of the Caradocian shelly facies is undoubtedly that of Bancroft who, by using mainly morphological changes in the trinucleid trilobites and the dalmanellaceid and strophomenaceid brachiopods, effected a correlation of critical sections in England and Wales. The results of his studies are set out in a privately published paper (Bancroft 1933)



and again, with some emendation of his earlier conclusions (1945 : 181-186) ; they include the division of the Caradoc Series into seven stages based upon successions exposed in Shropshire, an arrangement that has been admirably reviewed by Dean (1958). The chief impression one gets from Bancroft's publications, apart from an appreciation of his ingeniously analytical use of morphological detail in separating species, is one of stratigraphical precision. There is a lavish use of zones complete with index fossils ; faunas of supposed correlative significance are recorded from sections often measured to the nearest inch : and discontinuities in the records of various stocks are filled in by linear interpolations between known occurrences. In effect, either as a consequence of his researches, or as a reflection of the principles by which he worked, his final paper (Bancroft 1945) is a striking confirmation of the ubiquity of fossil assemblages and the orthogenetic nature of evolution (see his accounts of the derivation of the dalmanellids and strophomenids, pp. 189-190, 202-203, etc.).

It is therefore not surprising to find that Bancroft experienced no difficulty in applying the stages of the standard successions in Shropshire to the Caradoc rocks of Bala (Text-fig. 3). Indeed, the only faunal difference he considered noteworthy (1945 : 247) is that *Kjaerina*, which is so characteristic of the Longvillian Stage of east Shropshire, becomes less common westwards and is unknown in north Wales. But complications are far greater than this sole comment suggests. Accepting for the moment his conclusion that the Caradocian rocks of Bala belong to the stages Harnagian to Longvillian inclusive, thirteen out of the forty-two genera found in them have not been recorded from their Shropshire correlatives (Dean 1958 : 193-231) and ten Shropshire genera within that stratigraphical range, including such important stocks as *Harknessella*, *Marionites* and *Smeathenella*, are absent from Bala. Moreover only a few specifically indeterminable moulds of *Bancroftina*, *Horderleyella*, *Hedstroemina* and *Kjaerina* have been recovered from the Bala sediments ; while another stratigraphically important stock, *Dalmanella*, which occurs only fairly often in the Gelli-grîn Group has proved specifically distinct from all other described forms (contrary to Bancroft's identification of it as *D. horderleyensis* (1945 : 193) and *D. indica* (1945 : 195)). In fact, only five out of the twenty-three genera found in both regions are at present known to be represented by conspecific forms. They are *Bicuspina spiriferoides* (Lower Longvillian), *Heterorthis retrorsistria* (Soudleyan), *Howellites antiquior* (Lower Longvillian), *Onniella* cf. *soudleyensis* (Soudleyan) and *Reuschella horderleyensis* (Soudleyan), all of which, according to Bancroft and Dean, have a restricted range in Shropshire (indicated by the stage name following each species).

The low proportion of species common to both areas requires some comment. Such widespread species might be inadequate for purposes of correlation because they may have been less susceptible to morphological change than, for example, *Dalmanella* or *Macrocoelia* and are therefore more likely to have a greater stratigraphical range. This is probably true of *B. spiriferoides* which occurs throughout the Allt Ddu and Gelli-grîn Groups in contrast to its brief appearance in Shropshire. On the other hand the proportion may be low because, although the Caradocian



brachiopod faunas of Shropshire are generally regarded as having been well studied, there are a surprising number of undescribed stocks including fifteen (Dean 1958: 218-225) that are at least congeneric with Bala contemporaries and these may ultimately prove to be more helpful for correlation than the so-called index fossils. In the meantime I am inclined to place a great deal of reliance on *H. antiquior* and *H. retrorsistria* both of which have such a restricted range in the Bala district that one is tempted to regard their incoming as coincident with their incursion into the Shropshire province. Two other species, first described from the Welsh

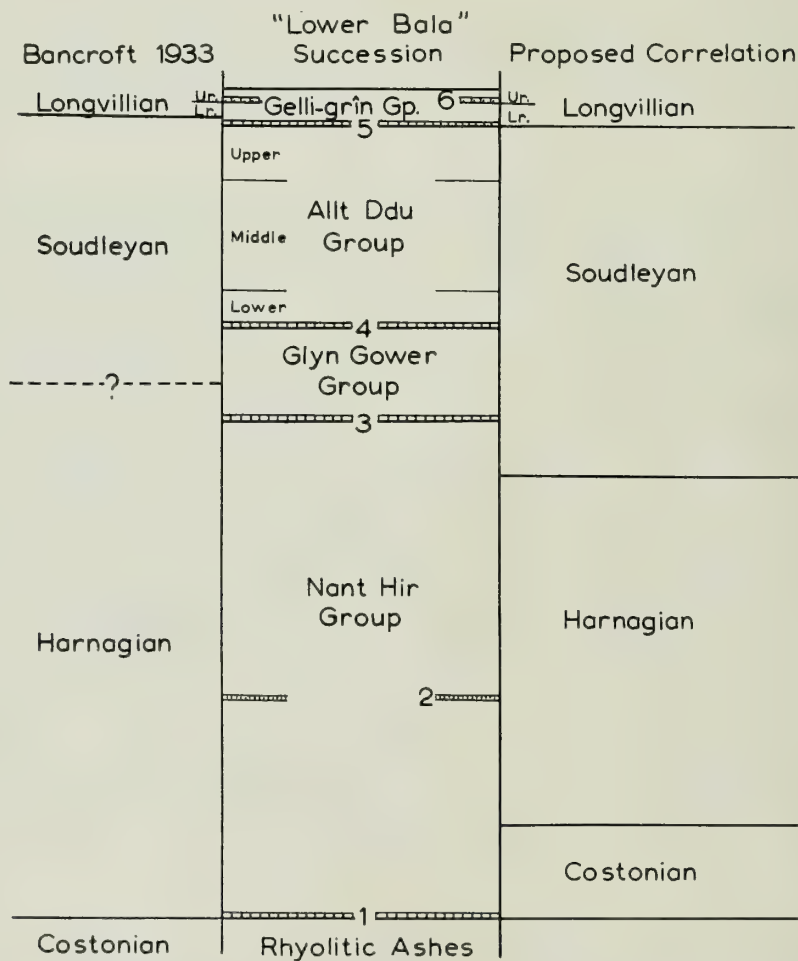


FIG. 3. The correlation of the Caradocian rocks of the Bala district according to Bancroft (1933) and the present study : 1, represents the Derfel Limestone ; 2, the fossiliferous horizon at Cefn-y-maes ; 3, the Cefn Gwyn Ash ; 4, the Frondderw Ash ; 5, the Pont-y-Ceunant Ash and 6, the Gelli-grin Limestone.



Borderlands, namely *Dinorthis berwynensis* and *Leptestiina oepiki*, also have a fairly restricted occurrence in the Bala succession. The former is known from the Llanyblodwel beds of Montgomeryshire where, like its Bala relative, it is associated with *H. retrorsistria*; the latter occurs in the Pen-y-garnedd Limestones that immediately succeed sandstones with an undoubted Lower Longvillian fauna (Whittington 1938a : 450). They confirm that the Upper Glyn Gower-Lower Allt Ddu Groups and the Gelli-grîn Group probably represent at least part of the Soudleyan and Lower Longvillian respectively. The location of the boundary between these two stages within the Bala succession is mainly a matter of convenience but since *Howellites antiquior* and *Leptestiina oepiki* appear first at the base of the Pont-y-Ceunant Ash, this member may be taken as the lowest constituent of the Longvillian. The base of the Soudleyan is even more indeterminate. A majority of the Nant Hir brachiopods was taken from a small thickness of mudstones about 1,700 ft. above the Derfel Limestone and only one of them, *Onniella* cf. *soudleyensis*, is at present also recorded in the rocks of the Welsh Borderlands. This species is found in the Soudleyan (Bancroft 1945 : 211) but the full ranges of early Caradocian *Onniella* are not well known and Professor Whittington's conclusion that the associated trilobites are on balance indicative of the Harnagian Stage, is more acceptable. The Harnagian-Soudleyan boundary is therefore probably somewhere above this horizon and may be taken as coincident with the first appearance of *Dinorthis berwynensis* and *Reuschella* cf. *horderleyensis*, i.e. just below the base of the Glyn Gower Group.

The correlation of the Derfel Limestone and the Upper Gelli-grîn ashes, which constitute respectively the base and the top of the Caradocian succession in the Bala area, is controversial for reasons that will become clear. On trilobite evidence, and particularly the presence of *Broeggerolithus* cf. *harnagensis* (Whittington 1955 : 420), the Derfel Limestone is usually regarded as being of Harnagian age. The large brachiopod fauna however, which is almost entirely unknown in Shropshire, is highly distinctive and is found in Anglesey in association with *Nemagraptus gracilis* and other diagnostic graptolites. Since this graptolitic fauna is too important to ignore, the basal member of the Nant Hir Group is best assigned to the Costonian stage.

The correlation of the terminal members of the Gelli-grîn Group has been affected by Bancroft's claim to have identified a widespread faunal break within the Longvillian. This is a recurrent theme in his papers. In 1933 he recorded a hiatus within the Lower ashes of the Gelli-grîn Group; later (Bancroft 1945 : 185) he spoke of a "prolonged hiatus at the base of the [Upper Longvillian] substage" which he identified in the Bala district as coincident with the base of the Gelli-grîn Limestone; and he implied in his discussion of the Caradocian faunas (pp. 182, 183) that there is palaeontological evidence for it. In order to show the size of this faunal break, the distribution and relative frequencies of the brachiopods found in the highest Caradocian rocks of Bala are given below where

- 1, represents the top of the Allt Ddu Group (twenty-one localities);
- 2, the Pont-y-Ceunant Ash (eight localities);



- 3, the lowest fifty feet of the lower calcareous ashes (twenty-five localities) ;
- 4, the middle part of the lower calcareous ashes with *Kloucekia apiculata* (M'Coy) (seventeen localities) ;
- 5, the lower calcareous ashes with *Chasmops* sp., immediately below the Gelli-grin Limestone (six localities) ;
- and 6, the upper calcareous ashes succeeding the Gelli-grin Limestone (eight localities).

The letters indicating the frequency of various species have been compiled as a percentage occurrence in localities for each horizon with rare (r) denoting 0-25% occurrence, fairly common (fc) 26-50%, common (c) 51-75% and very common (vc) 76% or more. The species known from the Gelli-grin Limestone at the type locality are prefixed by an asterisk.

|                                                               | 1  | 2  | 3  | 4  | 5  | 6  |
|---------------------------------------------------------------|----|----|----|----|----|----|
| <i>Bancroftina</i> sp. . . . .                                | —  | —  | —  | —  | —  | r  |
| <i>Bellimurina incommoda</i> sp. nov. . . . .                 | —  | —  | r  | r  | fc | r  |
| <i>Bicuspina spiriferoides</i> (M'Coy) . . . . .              | c  | vc | c  | fc | fc | r  |
| <i>Cremnorthis parva</i> gen. et sp. nov. . . . .             | —  | —  | —  | —  | —  | r  |
| <i>Cyclospira</i> sp. . . . .                                 | —  | r  | r  | r  | —  | —  |
| * <i>Dalmanella modica</i> sp. nov. . . . .                   | —  | fc | fc | fc | fc | r  |
| <i>Dinorthis berwynensis angusta</i> subsp. nov. . . . .      | c  | r  | —  | —  | —  | —  |
| * <i>Dolerorthis duftonensis proluxa</i> subsp. nov. . . . .  | —  | —  | fc | c  | vc | vc |
| <i>Dolerorthis</i> sp. . . . .                                | r  | —  | —  | —  | —  | —  |
| * <i>Eoplectodonta</i> cf. <i>rhombica</i> (M'Coy) . . . . .  | —  | vc | vc | c  | c  | vc |
| <i>Glyptomena</i> cf. <i>osloensis</i> (Spjeldnaes) . . . . . | —  | —  | —  | —  | r  | —  |
| <i>Howellites antiquior</i> (M'Coy) . . . . .                 | —  | c  | vc | vc | vc | r  |
| <i>Howellites ultima</i> Bancroft . . . . .                   | vc | —  | —  | —  | —  | —  |
| <i>Kiaeromena</i> cf. <i>kjerulfi</i> (Holtedahll) . . . . .  | r  | —  | —  | —  | —  | —  |
| * <i>Leptaena ventricosa</i> sp. nov. . . . .                 | c  | c  | fc | fc | c  | r  |
| * <i>Leptestiina oepiki</i> (Whittington) . . . . .           | —  | r  | r  | fc | vc | fc |
| <i>Lingulella</i> cf. <i>ovata</i> (M'Coy) . . . . .          | —  | —  | —  | r  | —  | r  |
| <i>Lingulella</i> cf. <i>tenuigranulata</i> (M'Coy) . . . . . | —  | —  | —  | r  | —  | —  |
| <i>Macrocoelia prolata</i> sp. nov. . . . .                   | c  | fc | fc | r  | —  | fc |
| * <i>Nicolella actoniae obesa</i> subsp. nov. . . . .         | —  | r  | fc | fc | c  | vc |
| <i>Onniella ostentata</i> sp. nov. . . . .                    | —  | fc | r  | r  | —  | r  |
| <i>Orbiculoidea</i> sp. . . . .                               | —  | —  | —  | —  | —  | r  |
| <i>Orthambonites cessata</i> sp. nov. . . . .                 | —  | —  | r  | r  | —  | —  |
| <i>Oxoplectia</i> sp. . . . .                                 | —  | —  | r  | —  | —  | —  |
| <i>Paracraniops macella</i> gen. et sp. nov. . . . .          | —  | —  | r  | r  | —  | —  |
| <i>Pseudocrania</i> cf. <i>divaricata</i> M'Coy . . . . .     | —  | —  | r  | —  | —  | —  |
| <i>Platystrophia</i> cf. <i>sublimis</i> Öpik . . . . .       | —  | fc | r  | r  | —  | —  |
| <i>Reuschella horderleyensis undulata</i> subsp. nov. . . . . | vc | c  | fc | r  | —  | c  |
| <i>Rhactorthis crassa</i> gen. et sp. nov. . . . .            | —  | —  | —  | r  | r  | r  |
| <i>Rostricellula sparsa</i> sp. nov. . . . .                  | r  | —  | —  | —  | —  | —  |
| <i>Salopia</i> sp. . . . .                                    | —  | r  | —  | —  | —  | —  |
| <i>Sericoides</i> sp. . . . .                                 | —  | —  | —  | —  | —  | r  |
| * <i>Skenidioides</i> cf. <i>costatus</i> Cooper. . . . .     | —  | r  | fc | fc | fc | r  |
| <i>Sowerbyella musculosa</i> sp. nov. . . . .                 | fc | —  | —  | —  | —  | —  |
| <i>Strophomena</i> sp. . . . .                                | —  | —  | r  | r  | fc | —  |



From the list, it is clear that the so-called break at the base of the Gelli-grîn Limestone does not exist and that although ten new species were introduced into the area during the deposition of the Pont-y-Ceunant Ash, important remnants of the Upper Allt Ddu fauna persisted and even more new species appeared within the lower calcareous ashes. As far as correlation is concerned the brachiopods are singularly unhelpful. Seventeen out of the twenty-eight genera found in the Gelli-grîn Group have not been recorded from either substage of the Shropshire Longvillian and only the sudden rarity of *H. antiquior* in the upper calcareous ashes, after its prolific occurrence in the lower beds, suggests that the youngest members of the Gelli-grîn Group belong to the Upper Longvillian.

The most disappointing aspect of this study is the failure to identify detailed subdivisions of the Shropshire Caradocian in an area that is only fifty miles distant. Indeed the differences between the two brachiopod faunas are so profound that even the use of the stages proposed by Bancroft calls for a number of compromises and the possibility that we are really comparing the fossil remnants of what were once two distinct benthic provinces must now be considered.

The most obvious feature of the brachiopod faunas recovered from the Caradocian rocks of Bala is the relative richness of the Derfel Limestone and Gelli-grîn assemblages. Between them they include all but four of the genera recorded in the district and the exceptions—*Hedstroemina*, *Heterorthis*, *Rostricellula* and *Vellamo*—together with twelve other genera are all that are found in the intervening four thousand feet of strata. There is also some relationship between these two assemblages in that certain genera, *Dolerorthis*, *Eoplectodonta*, *Leptestiina*, *Nicolella*, *Oxoplecia*, *Platystrophia* and *Salopia*, are common to them both but unknown from the rest of the succession, while *Onniella* and *Sericoidea* are additionally recorded only from the Nant Hir. Not one of these recurring genera however, is represented by the same species and if the two assemblages indicate briefly occurring intrusions into the Bala environment of a fauna belonging to another province, then the composition of that fauna changed generically as well as specifically during the intervening period. Thus *Anisopleurella*, *Cyrtonotella*, *Glossorthis*, *Orderleyella*, *Kjaerina*, *Kullervo* and *Palaeostrophomena* are limited to the Derfel Limestone; while *Bellimurina*, *Cremnorthis*, *Cyclospira*, *Glyptomena*, *Orthambonites*, *Paracraniops*, *Pseudocrania*, *Rhactorthis*, *Skenidioides* and *Strophomena* are exclusive to the Gelli-grîn Group. The most intriguing aspect of such a fauna is its strong Baltic affinities (Whittington & Williams 1955 : 398–402) and it is proposed to refer to it as the *Nicolella* association on the understanding that its principal elements are those stocks common to both the Derfel Limestone and the Gelli-grîn Group, supplemented by less persistent associates like those listed above but excluding at least *Sericoidea* and *Onniella*.

The remaining genera, limited though they are in numbers, also show some interesting relationships. *Dinorthis*, *Macrocoelia* and *Reuschella*, with rare *Dalmanella* and *Hedstroemina*, first appear in the Glyn Gower Group and these three, except for the absence of *Dinorthis* from the Middle Allt Ddu and its disappearance just above the base of the Pont-y-Ceunant Ash, thereafter persist throughout the Caradocian successions of the Bala district. Just above the Frondderw Ash these



stocks are joined by *Heterorthis*, which occurs in brief profusion, *Leptaena* and *Bicuspina*, both of which reappear in the Upper Allt Ddu to continue through into the Gelli-grîn Group. *Dinorthis*, *Leptaena*, *Heterorthis* and *Bicuspina* then were subject to vacillating occurrences within the Caradocian succession in the manner of the *Nicolella* association and may be referred to as the *Dinorthis* association: the genera *Heterorthis* and *Bicuspina*, are known from the Llandeilian rocks of Bohemia. A third association remains to be described; it includes *Howellites*, which first appeared in the Derfel Limestone but is pre-eminently characteristic of the Allt Ddu and Gelli-grîn Groups, *Sowerbyella* which occurs throughout all Groups except the Gelli-grîn, and rare ancillary members like *Rostricellula*. The *Howellites* association to which *Macrocoelia* and *Reuschella* are more appropriately relegated, is interesting in that the ancestral stocks of its members are known from the pre-Caradocian rocks of the Anglo-Welsh area and it may therefore be regarded as the chief indigenous group in the Bala assemblages.

Whether these three associations represent remnants of biotic communities that existed in a north Welsh province during Caradocian times is a matter for further exploration. Their heterogeneity at first seems to be against it. The simultaneous appearance of *Leptestiina*, *Nicolella*, *Platystrophia*, etc. at the base and the top of the Caradocian succession in the Bala district is noteworthy and although they occur with different stocks and as distinct species, such differences can reasonably be attributed to replacement and speciation during the intervening period. *Howellites* and *Sowerbyella* however, the two principal members of the supposed indigenous association which occur throughout the Allt Ddu Group, can be referred to five species, *H. striata* Bancroft, *H. intermedia* Bancroft and *H. ultima* Bancroft, *S. sericea permixta* subsp. nov. and *S. musculosa* sp. nov. Had the collections examined been samples of an evolving community in continuous occupation of the Allt Ddu silts, specific differences would have been expected to arise phylogenetically like the change in radial ornamentation of *Howellites* described by Bancroft (1945: 204). In fact those trends proved not to be valid, and, when the variability of other characters is taken into account, there are better reasons for believing the three *Howellites* species to have been contemporary stocks, each in turn playing its part in a continual colonization of the silty environment then extant. Similar relationships exist between the two *Sowerbyella* species. *S. sericea permixta* persisted throughout the Nant Hir and Glyn Gower Groups into the Allt Ddu but was replaced by the unrelated *S. musculosa* towards the top of that Group.

Even within associated generic stocks therefore, there seems to be good evidence for replacement and transposition at the specific level. None the less it is probably significant that the *Nicolella* association is found in the only two suites of calcareous sediments within the Bala succession, whereas the *Dinorthis* and *Howellites* associations are pre-eminently characteristic of the sandier and muddier beds respectively.

The existence of such facies controls can, to some extent, be demonstrated in the following manner. Fifty-seven genera of brachiopods have been recorded from the Caradocian deposits of England and Wales ranging in lithology from limestones to mudstones and conglomerates. Ignoring the genera *Bancroftina*, *Dolerorthis*,



*Lingulella*, *Macrocoelia* and *Sowerbyella*, which have been taken from every kind of sediment, and *Anisopleurella*, *Bellimurina*, *Cremnorthis*, *Cryptothyris*, *Cyclospira*, *Cyrtonotella*, *Glossorthis*, *Glyptorthis*, *Heterorthina*, *Kiaeromena*, *Kjerulfinia*, *Kullervo*, *Marionites*, *Orthambonites*, *Orthorhynchula*, *Palaeostrophomena*, *Paterula*, *Philhedra*, *Pseudocrania*, *Ptychoglyptus*, *Skenidioides* and *Triplesia* which are at present known only from one particular horizon in one area, a residuum of twenty-nine genera is left. The incidence of species belonging to these genera in six different lithologies is given below where :

1, represents limestones ;

2, calcareous sandstones ;

3, sandstones and grits ;

4, siltstones ;

5, mudstones and shales ;

and 6, calcareous mudstones.

The data have been compiled from the papers of Bancroft (1933, 1945), Whittington (1938, 1938a), Dean (1958, 1959) as well as from the present study so that there is a fairly wide coverage of both lithology and locale : and a clear preponderance of species for any one genus in a particular lithology is indicated by an asterisk.

|                                | 1 | 2 | 3 | 4 | 5 | 6 |
|--------------------------------|---|---|---|---|---|---|
| <i>Bicuspinga</i> . . . . .    | — | x | * | x | — | x |
| <i>Dalmanella</i> . . . . .    | — | * | x | x | x | x |
| <i>Dinorthis</i> . . . . .     | — | x | * | x | x | x |
| <i>Eoplectodonta</i> . . . . . | — | x | — | x | — | * |
| <i>Harknessella</i> . . . . .  | x | x | x | x | — | — |
| <i>Hedstroemina</i> . . . . .  | — | — | — | * | — | — |
| <i>Heterorthis</i> . . . . .   | x | x | * | x | — | x |
| <i>Horderleyella</i> . . . . . | — | x | * | x | — | x |
| <i>Howellites</i> . . . . .    | — | x | x | * | x | — |
| <i>Kjaerina</i> . . . . .      | x | * | — | x | x | x |
| <i>Leptaena</i> . . . . .      | — | * | * | x | — | x |
| <i>Leptestiina</i> . . . . .   | — | x | — | x | — | * |
| <i>Nicolella</i> . . . . .     | x | x | — | x | — | * |
| <i>Onniella</i> . . . . .      | — | x | — | x | * | x |
| <i>Orbiculoidea</i> . . . . .  | x | * | x | x | — | x |
| <i>Oxoplectia</i> . . . . .    | — | x | x | x | — | x |
| <i>Paracraniops</i> . . . . .  | — | — | — | x | x | * |
| <i>Platystrophia</i> . . . . . | x | x | — | x | — | * |
| <i>Reuschella</i> . . . . .    | — | x | x | x | x | x |
| <i>Rhactorthis</i> . . . . .   | — | * | — | x | — | x |
| <i>Rostricellula</i> . . . . . | — | — | * | x | — | — |
| <i>Salopia</i> . . . . .       | — | x | x | x | — | x |
| <i>Schizocrania</i> . . . . .  | x | — | — | x | x | x |
| <i>Servicoidea</i> . . . . .   | — | — | — | x | * | x |
| <i>Siphonotreta</i> . . . . .  | — | x | x | x | — | — |
| <i>Smeathenella</i> . . . . .  | — | x | x | x | — | — |
| <i>Strophomena</i> . . . . .   | x | x | — | x | — | * |
| <i>Trematis</i> . . . . .      | x | — | — | x | x | x |
| <i>Vellamo</i> . . . . .       | — | — | x | * | — | — |



Most of the genera are obviously tolerant of many lithological environments, a reflection no doubt of species adaptation, but some of the patterns are worth noting. The preferred environment is undoubtedly the silty bottom which supported species of every genus listed. *Onniella*, *Sericoidea* and *Paracraniops* are especially characteristic of the muddy environment : but above all, the list confirms the prevalence of the *Nicolella* association (with *Eoplectodonta*, *Leptestiina*, *Platystrophia*, *Rhactorthis*, and *Strophomena*) in a lime-rich environment and of the *Dinorthis* association (with *Bicuspina*, *Dalmanella*, *Heterorthis* and *Leptaena*) in a sandy substratum. In this context the diachronism of faunas, implicit in Bancroft's correlations, is to be expected. Thus the *Nicolella* association appeared during Lower Longvillian times in the Bala district, in Upper Longvillian times in the Berwyn Hills, but not until Marshbrookian-Actonian times in South Shropshire. In contrast, the *Dinorthis* association, with the possible exception of *Bicuspina*, is present in the sandy Costonian facies of Shropshire but did not reach the Bala region until Soudleyan times when the coarser Glyn Gower beds were being deposited.

### III. SYSTEMATIC DESCRIPTIONS

OBOLACEA King 1846

OBOLIDAE King 1846

LINGULELLINAE Schuchert 1893

**LINGULELLA** Salter 1866

TYPE SPECIES. *Lingula davisii* M'Coy by subsequent designation of Dall (1870 : 159).

***Lingulella cf. ovata*** (M'Coy)

(Pl. 1, figs. 1-3)

The impressions of a few lingulids have been recovered from the Caradoc rocks of the Bala district, especially from those assigned to the Gelli-grŷn Group, and the external and internal moulds of a pedicle valve, (BB.28985-86) from coarse calcareous ashes exposed 400 ft. east-south-east of Bryn-briglas Farm, have been figured to illustrate their close resemblance to *Lingulella ovata* (M'Coy 1846 : 24). The valve, which was 18 mm. long, 11.5 mm. wide and about 3 mm. deep, was elongately oval in outline with subparallel lateral margins and evenly convex in longitudinal and transverse profiles. The external surface was ornamented by closely set, fine, raised, concentric ridges grouped at about 6 to 7 per mm. at 10 mm. antero-medianly of the umbo. The postero-median area is not well preserved and no details of the ventral interior around the beak are known, but another internal mould of a dorsal valve (BB.28987), from calcareous ashy mudstones of the Gelli-grŷn Group exposed above the limestone in the old quarry 500 ft. west-south-west of Gelli-grŷn Farm, which can probably be allocated to the same stock, shows the trace of a short median ridge extending anteriorly from the umbonal region for about 5 mm.



In outline and ornamentation the specimens are certainly very like *L. ovata*, and although the pedicle valve may prove to be significantly deeper, more material will have to be obtained to determine whether this difference is systematically important.

CRANIACEA Gray 1840

CRANIIDAE Gray 1840

*Pseudocrania* M'Coy 1851

TYPE SPECIES. *Crania antiquissima* Verneuil by original designation of M'Coy (1851 : 387).

*Pseudocrania* cf. *divaricata* M'Coy

(Pl. 1, figs. 4, 5 ; Text-fig. 4)

Deformed external and internal moulds, about 21 mm. long, of a brachial valve (BB.28988–89), of *Pseudocrania* have been collected from calcareous ashes of the Gelli-grîn Group exposed immediately west of the fence at the south-east end of the Rhiwlas Limestone scarp, about 500 ft. south-west of B.M.1338.7, Bryn Pig. The exterior of the valve was gently convex, about one-tenth as deep as long with the apex located near the straight posterior margin ; the anterior part of the commissure was slightly emarginate. The surface of the external mould is not well preserved but here and there, especially peripherally, there occur impressions of radiating, rounded costellae numbering about 3 per mm. In contrast, the fine details of the internal mould permit a full reconstruction of the dorsal musculature and the mantle (Text-fig. 4). The elliptical anterior adductor scars, inserted on either side of a low median ridge about half way along the valve from the posterior margin, are the most conspicuous muscle set in the manner typical of *Pseudocrania*. Anteriorly and antero-medially to them, on a slightly raised triangular platform, occur respectively a rather widely spaced pair of elevator scars and a smaller subjacent pair of protractor scars. The unpaired median muscle occupied a small depression which indented the thickened posterior margin to the valve, and lateral to it the posterior adductor and the oblique internal scars can be made out. The pallial sinus pattern within the mantle appears to have consisted of a pair of *vascula media* which branched into three main canals as they emerged from the visceral chamber anterior of the anterior adductor bases, and a pair of arcuate, highly branched *vascula genitalia* originating lateral of the posterior adductors.

The specimens are very close in morphology to those figured by Davidson (1866, pl. 8, figs. 7–12) as *Crania divaricata* (M'Coy) and especially to a dorsal internal mould from the Chair of Kildare (pl. 8, fig. 11a) which also possesses the impression of a triangular platform in front of the anterior adductor impressions. Indeed the only noteworthy contrast is the relatively small size and shallowness of the posterior adductor impressions of the Welsh internal mould, and until more is known about the systematic importance of this difference, the moulds are best compared with M'Coy's species.



## Family CRANIOPSIDAE nov.

Subequivalve, unattached craniaceids (?) usually with well defined platforms of secondary shell substance bearing muscle impressions ; shell substance impunctate.

Genus *PARACRANIOPS* nov.

DIAGNOSIS. Oval, subequivalve shells with apices of both valves located at or near posterior margins ; external surfaces ornamented by well developed but sporadically occurring lamellae eccentric about apices of valves ; ventral (?) interior with subcircular to subtriangular raised area culminating in low eminence posteriorly but broken anteriorly by median depression, that possibly accommodated the oblique internal muscle bases, and containing anteriorly a pair of suboval impressions, interpreted as scars of anterior adductors ; elongate impressions outside

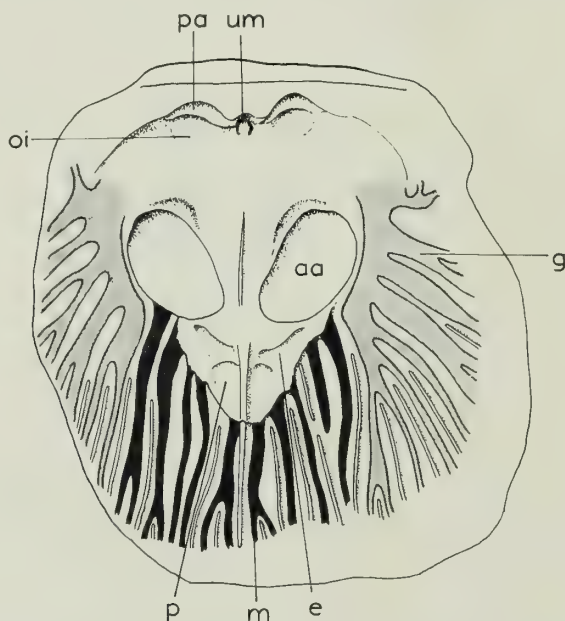


FIG. 4. An interpretation of the impressions found in the dorsal interior of *Pseudocrania* cf. *divaricata* M'Coy,  $\times 3.5$  approx.: aa, anterior adductor scar ; e, elevator scar ; g, vascula genitalia ; m, vascula media ; oi, oblique internal scar ; p, protractor scar ; pa, posterior adductor scar ; um, unpaired median scar.

postero-lateral flanks of raised area probably represent posterior adductors ; dorsal (?) interior with pair of low ridges commonly widely splayed about small, postero-median eminence, narrowly elongate indentations parallel with and posterior to ridges, and pair of larger, suboval, impressions antero-lateral to them and separated by broad median band probably represent dorsal posterior and anterior adductor scars respectively ; shell substance calcareous, impunctate.



TYPE SPECIES. *Craniops* ? *pararia* Williams (1962) from the Kiln Mudstones, Craighead.

DISCUSSION. When the species *Craniops* ? *pararia* was first described (Williams 1962 : 88) it was pointed out that the internal morphology was so different from that of *C. squamiformis* (Hall), the type species of *Craniops*, or any other Silurian and Devonian stock that its inclusion in the genus *Craniops* was only provisional. Since then additional material from Craighead and also internal and external moulds from the Bala district have shown that the differences are indeed important.

The chief difficulty in assessing the taxonomic importance of morphological changes in extinct fossil groups arises from the uncertainty over their anatomical significance and the craniopids, lacking as they do any obvious affinities with other, better known brachiopods, are no exception. Cooper (1956 : 236) has classified them as trimerellaceids, and included them in the Paterulidae. In the Russian Treatise on Brachiopoda (Gorjansky 1960 : 177), they have been assigned to the craniaceids. This allocation seems preferable because they do bear some resemblance to certain free-living craniids like *Pseudocrania* in the lack of a pedicle opening and

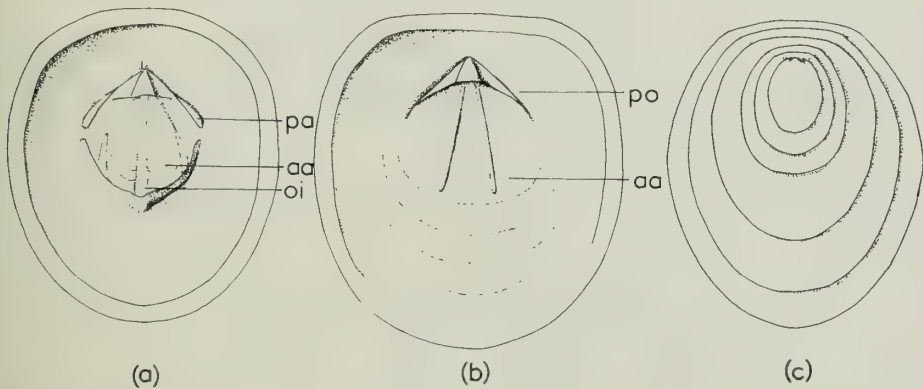


FIG. 5. The ventral ? (a) and dorsal ? (b) interiors and dorsal exterior (c) of *Paracraniops pararia* (Williams),  $\times 5$  approx.: aa, anterior adductor scar ; oi, oblique internal scar ; pa, posterior adductor scar ; po, posterior adductor and oblique internal scars.

in the possession of a calcareous shell, although both these characters could well have arisen independently ; and the absence of caeca penetrating the shell in the manner of the craniaceids may reflect such a process. None the less there are certain indentations on the floors of both valves that can confidently be taken as the scars of muscle attachments (Text-fig. 5). Two well-defined pairs in both valves probably represent the seats of attachment of the adductor bands, and, provided the apices of the valves point posteriorly, may be homologized with the posterior and anterior sets of the craniaceids. In addition to these, the more elaborate platform of one of the valves, is deeply indented antero-medianly and if this is the area once occupied by the oblique internal muscles then this valve is the "ventral" or "pedicle" and its counterpart the "dorsal" or "brachial". If this is so, the elongate impressions



lying posterior to the ridges in the dorsal valve may represent the seats for the dorsal ends of the oblique internal muscles as well as the posterior adductors. For this reason alone the designation of the valves is the reverse of that put forward previously (Williams 1962) but it is still, of course, a matter of inference and cannot be accepted with certainty.

Having orientated the shell it is now possible to discuss the difference among the new genus, *Craniops* Hall 1859 (*Pholidops* Hall 1859 is a junior homonym) and *Pseudopholidops* Bekker 1921 which relate entirely to internal features. In the ventral (?) valve of *Craniops*, a central subtriangular platform pointing anteriorly is well developed so that the raised antero-median ridge, presumably for the reception of the ventral ends of the oblique internal muscles, contrasts with the median indentation, within the differently shaped raised area, of the new genus. The ventral posterior adductor scars are also differently located for in *Craniops* they are so widely separated as to form conspicuous, subcircular impressions at the ends of the base to the main platform. In the dorsal (?) valve the differences are even more striking because an elaborate platform containing both sets of adductor scars is characteristic of *Craniops* in contrast to the pair of widely divergent ridges separating the two adductor sets as in *Paracraniops*.

The species included by Bekker (1921 : 64-66) within his genus *Pseudopholidops* have a variable internal morphology but are immediately distinguishable from those assigned to *Paracraniops* in possessing three discrete pairs of muscle scars in the dorsal valve. Only one ventral interior has been described, that of *Pseudopholidops complicata* Bekker (1921 : 66), but this is also quite different in the extreme posterior location of the posterior adductors and also in the presence of a split ridge postero-medianly.

Apart from the type species, *Craniops trentonensis* (Hall 1866), *Craniops minor* (Winchell & Schuchert 1893), *Craniops attenuata* Cooper 1956 and *Craniops tenuis* Cooper 1956, all from Mohawkian rocks of N. America, probably belong to the new genus, although at present the interiors of these species are unknown. *Paracraniops macella* sp. nov. from the Caradocian rocks of Bala and "*Pholidops*" *infrasilurica* Huene 1899, *P. estona* Bekker 1921 and *P. elegans* Bekker 1921 from the mid-Ordovician of the Baltic region are only provisionally included because they differ from the Scottish and American stocks in the terminal location of the apices of the valves and also in the absence of the postero-median eminence in the dorsal valve.

***Paracraniops macella* gen. et sp. nov.**

(Pl. I, figs. 6-8)

**DIAGNOSIS.** Elongately oval subequivalve *Paracraniops* with valves just over three-quarters as wide as long measured between a slightly flattened posterior margin and a strongly curved anterior one, ventral (?) valve slightly more convex, apices acute terminal; lamellose ornamentation strongly developed, becoming widely spaced antero-medianly; ventral (?) interior with subcircular platform, less than two-thirds as long as valve, containing antero-laterally a pair of suboval adductor impressions and broken antero-medianly by a long depression presumably



the median oblique internal scar, posterior adductors elongate, flanking low posterior edges of platform ; dorsal (?) interior with poorly developed ridges widely extended about a low posterior eminence, anterior adductor scars impressed antero-laterally within a vaguely defined raised border extending anteriorly for about one-half the length of the valve.

|            |                                                   |               |                    |
|------------|---------------------------------------------------|---------------|--------------------|
| HOLOTYPE.  | Internal mould of ventral (?) valve<br>(BB.28990) | length<br>2.0 | width (mm.)<br>1.5 |
| PARATYPES. | External mould of ventral (?) valve<br>(BB.28991) | 1.7           | 1.4                |
|            | External mould of dorsal (?) valve<br>(BB.28992)  | 1.8           | 1.3                |
|            | Internal mould of dorsal (?) valve<br>(BB.28993)  | 1.8           | 1.4                |
|            | External mould of ventral (?) valve<br>(BB.28994) | 1.5           | 1.0                |
|            | External mould of dorsal (?) valve<br>(BB.28995)  | 1.9           | 1.5                |
|            | Internal mould of dorsal (?) valve<br>(BB.28996)  | 2.0           | 1.5                |

HORIZON AND LOCALITY. Calcareous ashes of the Gelli-grŷn Group exposed in a quarry at the side of the road leading to Y Garnedd, about 300 ft. south-east of that farm.

DISCUSSION. The moulds collected from the Gelli-grŷn Group may be separated immediately from Scottish and American *Paracraniops* in the terminal location of the apices of the valves although in this respect it resembles specimens described by Bekker (1921 : 62, pl. 2, figs. 4, 5) as *Pholidops estona*. Both stocks are also elongately oval but the new species may prove to be relatively wider (see Table 1) for the measurements given by Bekker suggest that *P. estona* was less than three-fifths as wide as long. The average length of the platform relative to the length of 4 ventral valves from Bala was 56.3% (variance 8.33) and, judging from Bekker's illustration, the ventral muscle platform of *P. estona* is similarly proportioned although within the anterior margin there also occurs a pair of curved ridges extending parallel with the margin from a central ring of shell, a structure not impressed in the Welsh moulds. In the dorsal interior of *P. estona* the anterior adductor scars are very much smaller and the posterior ridges are not obtusely splayed as in *Paracraniops macella*.

TABLE 1

|                          |   |   |        |           |
|--------------------------|---|---|--------|-----------|
| $\bar{l}$ mm. (var. l) . | . | . | 1.68   | (0.123)   |
| $\bar{w}$ mm. (var. w) . | . | . | 1.29   | (0.091)   |
| r .                      | . | . | 0.937  |           |
| a (var. a) .             | . | . | 0.8602 | (0.00821) |

TABLE 1. Statistics of maximum length (l) from posterior to anterior margins and maximum width (w) of 13 ventral (?) valves of *Paracraniops macella* sp. nov.



## Superfamily ACROTRETACEA Schuchert 1896

## Family DISCINIDAE Gray 1840

Genus **ORBICULOIDEA** D'Orbigny 1847

TYPE SPECIES. *Orbicula forbesii* Davidson 1848 (application pending under the Plenary Powers (*Bull. Int. Comm. Zoo. Nomencl.*, **19**, No. 5 [in Press]) : appeal by A. J. Rowell).

***Orbiculoidea* sp.**

(Pl. 1, fig. 9)

The interior of an incomplete brachial valve (BB.29135), taken from calcareous ashes exposed above the Gelli-grin Limestone in the old quarry just north of the track and 500 ft. west of Gelli-grin Farm, is all that has been found of the genus *Orbiculoidea* in the Caradocian rocks of Bala. The valve is eccentrically conical about an apex which is situated 1 mm. forward of the straight posterior margin, although it tends to flatten out about 2.5 mm. anterior of the apex. Judging from details of the interior, the external surface was ornamented by fine, closely spaced, concentric ridges and the valve was probably subcircular in outline. The only other internal feature worth noting is a faint, thin ridge extending antero-medially from the apex for about 1 mm.

Undescribed *Orbiculoidea* are known throughout much of the Caradocian of Shropshire (Dean 1958 : 218-222) and the Bala form may prove to be related to them, but more material will have to be obtained for any conclusive comparative study.

## Superfamily ORTHACEA Woodward 1852

## Family ORTHIDAE Woodward 1852

## Subfamily ORTHINAE Woodward 1852

Genus **ORTHAMBONITES** Pander 1830

TYPE SPECIES. *Orthambonites transversa* Pander by subsequent designation of Dall (1877 : 51).

***Orthambonites cessata* sp. nov.**

(Pl. 1, figs. 10-14)

DIAGNOSIS. Unequally biconvex subquadrate *Orthambonites* with high pedicle valve about one-third as deep as long and curved apsacline, ventral interarea almost one-quarter as long as valve ; brachial valve obscurely sulcate, over two-thirds as long as wide and nearly one-quarter as deep as long, dorsal interarea strong, curved anacline ; ornamentation consisting of about 15 subangular costae about 0.5 mm. in wavelength, 5 mm. anterior of the ventral umbo with delicate concentric lamellae ; strong teeth supported by receding dental lamellae, ventral muscle field subtriangular in outline about three-tenths as long as pedicle valve with pair of adductor scars,



not enclosed by diductor scars ; ventral pallial sinus pattern saccate, *vascula media* separated at their confluence with diductor submedian lobes by boss of secondary shell in adult shells ; cardinal process massive but undifferentiated, brachiophores extending antero-ventrally for less than one-quarter the length of brachial valve, as pair of divergent blades, rectangular in outline, sockets oval and deep, defined by secondary shell surrounding bases of brachiophores, median ridge strong, dorsal adductor field quadripartite, extending forward of dorsal umbo for over one-half the length of brachial valve and including subequal posterior and anterior adductor scars ; dorsal pallial sinus pattern poorly impressed, possibly digitate.

|            |                                                             | length | width (mm.) |
|------------|-------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of brachial valve (BB.28997)                 | 6.0    | —           |
| PARATYPES. | Internal mould of brachial valve (BB.29002)                 | 8.5    | 10.5        |
|            | Internal and external moulds of pedicle valve (BB.28998-99) | 9.0    | —           |
|            | Internal and external moulds of pedicle valve (BB.29000-01) | 6.5    | 8.0         |

HORIZONS AND LOCALITIES. Gelli-grîn Group : BB.28998-99, BB.29002 from calcareous ashes cropping out 400 ft. east-south-east of Bryn-briglas Farm ; BB.28997 from calcareous ashes exposed on Creigiau Bychain, 600 yds. north-east of Glyn-bach ; BB.29000-01 from calcareous ashes exposed at Myrddin Marad.

DISCUSSION. Rare moulds, referable to the genus *Orthambonites*, have been collected from rocks of the Gelli-grîn Group but are sufficiently distinctive to be described as a new species. The shell outline is subquadrate for although young shells tend to be widest along the hinge-line, lateral increment was accelerated during later stages of growth, and for four adult brachial valves the mean percentage length relative to maximum width, which was anterior of the hinge-line, was 70% (variance 90.7). Both valves were strongly and evenly convex in longitudinal profile due partly to the development of long interareas : the mean percentage thicknesses relative to lengths of three pedicle and three brachial valves were 32.3 (ranging between 30-34) and 24 (range 23-25) respectively. Despite the strong convexity of the brachial valve, the dorsal sulcus was vestigial amounting to no more than a slight median flattening involving the two submedian costae, and only discernible in transverse profile. The ornamentation consisted of 13, 14, 15 and 16 costae in 1, 0, 2 and 1 external ventral moulds, with an average wavelength of 0.57 mm. (range 0.5-0.7 mm.) 5 mm. antero-medially of the umbones of three pedicle valves.

The subtriangular ventral muscle field, which was deeply impressed on the floor of the pedicle valve, was about as long as wide in young valves, but during adult growth the anterior border expanded very much faster so that the mean percentage length relative to the length of four internal moulds was 30 (variance 11.67). The dorsal adductor muscle field was also well defined and its mean percentage length



relative to the length of four internal moulds was 58 (variance 12.67). But the cardinalia constituted the most distinctive features of the dorsal interior for the cardinal process was strongly developed even in young valves, almost filling the notothyrium as a thick, ventrally swollen shaft, and the brachiophores long and blade-like with an average percentage extension relative to the length of three internal moulds of 23 (range 18-27).

Apart from the high interareas which are not common attributes of described species of *Orthambonites* the two most distinctive features are the lack of a definite sulcus in a brachial valve that is so strongly convex and the long blade-like brachiophores reminiscent of those typical of *Hesperorthis*. A few known paucicostate species like *O. mostellerensis* Cooper and *O. rotundiformis* Cooper (1956 : 306, 311) are also feebly sulcate and the multicostate *O. brachiophorus* Cooper (1956 : 298) is equipped with similar brachiophores ; but in no other species are both these features found in combination.

Davidson (1869, pl. 35, figs. 1-3) figured three shells as *Orthis calligramma* Dalman which are more appropriately relegated to the genus *Orthambonites* as at present defined, and are purported to come from " Moelydd, near Bala ". These specimens together with others labelled as having been collected from the same locality are now preserved in the British Museum (BB.13455, BB.28840-48). They are all complete, undeformed shells or valves which could not have come from the Bala district ; some at least, judging from the adherent matrix as well as the external morphology of the shells, were almost certainly taken from the mudstones associated with the Craighead Limestones and are representatives of *Orthambonites playfairi* Reed (see Williams 1962 : 97).

#### Subfamily PRODUCTORTHINAE Schuchert & Cooper 1931

##### Genus *NICOLELLA* Reed 1917

TYPE SPECIES. *Orthis actoniae* J. de C. Sowerby by original designation of Reed (1917 : 860).

##### *Nicolella actoniae* (J. de C. Sowerby)

(Pl. 1, figs. 15-19 ; Text-fig. 6)

1839 *Orthis actoniae* J. de C. Sowerby : 639, pl. 20, fig. 16r, non fig. 16e.

DIAGNOSIS (emended). Large, plano- to slightly concavo-convex, subquadrate to mucronate *Nicolella* with evenly convex pedicle valve less than one-third as deep as long and short, curved, orthocline ventral interarea ; brachial valve commonly widest at hinge-line, almost two-thirds as long as wide with very short, curved anacline interarea ; ornamentation consisting of 11 to 15 angular costae, wavelength about 1 mm. at 5 mm. anterior of dorsal umbo, costellae not typically developed within 7.5 mm. of dorsal umbo but with 3ā usually arising earlier than 1ā, concentric lamellose outgrowths strong but irregularly disposed ; teeth strong, commonly striated, supported by short, receding dental lamellae, ventral muscle



field elongately oval in outline extending anterior of umbo for about two-fifths the length of valve, submedian lobes not enclosing lanceolate adductor impressions anteriorly ; ventral pallial sinus pattern saccate, *vascula media* closely adjacent posteriorly splayed and divided anteriorly ; cardinal process ridge-like and erect, flanked by chilidial plates, brachioophores short, widely splayed and together with notothyrial platform commonly heavily encased in secondary shell and united to short median ridge, dorsal adductor field small, obscured by proximal ends of *vascula myaria* and *media*, pallial sinus pattern saccate modified to digitate.

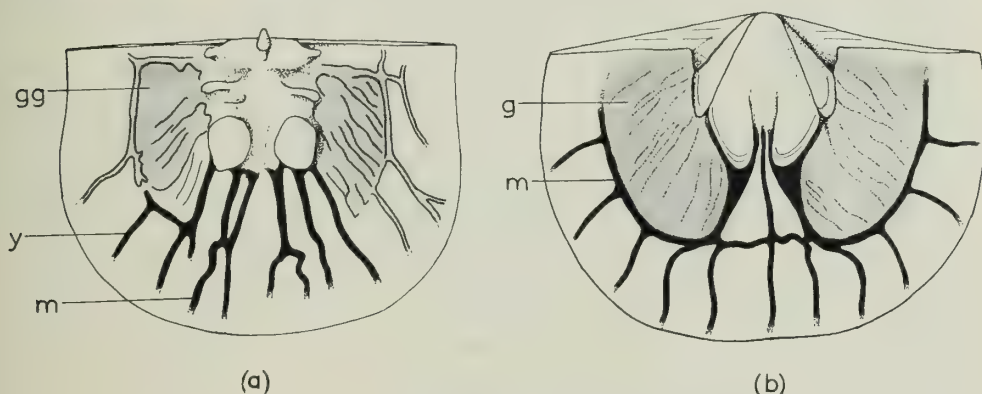


FIG. 6. The dorsal (a) and ventral (b) interiors of *Nicolella actoniae* (J. de C. Sowerby),  $\times 2.5$  approx., showing the pallial sinus patterns : *g*, impression of gonocoele ; *gg*, *vascula genitalia* ; *m*, *vascula media* ; *y*, *vascula myaria*.

|            |                                                                   | length | width (mm.) |
|------------|-------------------------------------------------------------------|--------|-------------|
| LECTOTYPE. | Internal mould of pedicle valve<br>(G.S.M. Geol. Soc. Coll. 6883) | 19.0   | 23.0        |
| OTHER      |                                                                   |        |             |
| MATERIAL.  | Internal mould of pedicle valve<br>(B.74772)                      | 17.8   | 29.5        |
|            | External mould of brachial valve<br>(BB.27315)                    | 18.3   | 24.8        |
|            | Internal mould of brachial valve<br>(BB.27317)                    | —      | —           |
|            | Internal mould of brachial valve<br>(BB.28959)                    | 16.0   | 21.0        |

HORIZON AND LOCALITIES. Actonian Stage : the lectotype, G.S.M. 6883 and B.74772 from buff-weathering sandstones, "Acton Scott", Shropshire ; BB.27315 and 27317 from buff-weathering sandstones exposed in a stream section by the east side of a road-bridge about 1,000 ft. west-south-west of Hatton, Shropshire ; BB.28959 from loose blocks near Acton Scott Church, possibly from the quarry of Castle Hill, one-third of a mile west-south-west of Acton Scott.



*Nicolella actoniae* J. de C. Sowerby *obesa* subsp. nov.

(Pl. 2, figs. 1-5, 7)

DIAGNOSIS. Plano- to slightly concavo-convex, mucronate *Nicolella* with highly convex pedicle valve over two-fifths as deep as long and short, curved, orthocline ventral interarea ; brachial valve widest at hinge-line, about three-fifths as long as wide, with short, curved, anacline interarea ; radial ornamentation interrupted by strong, irregularly developed, concentric lamellose outgrowths and consisting of 11 to 14 angular costae with wavelength of about 1 mm. at 5 mm. anterior of dorsal umbo, costellae fairly common within 7.5 mm. of dorsal umbo and with 3a usually originating before 1a ; teeth, commonly striated, supported by short, receding dental lamellae, ventral muscle field oval and extending anterior of umbo for about two-fifths the length of valve, submedian diductor lobes not enclosing lanceolate adductor impressions anteriorly ; ventral pallial sinus pattern saccate to lemniscate with closely situated *vascula media* dividing anteriorly ; cardinal process, erect and ridge-like flanked by chilidial plates ; brachiophores, short, widely divergent, extending on either side of median plane for about one-third of the length of hinge-line, and commonly ankylosed to short median ridge, by heavy deposits of secondary shell ; dorsal adductor field poorly impressed extending anteriorly for about one-third the length of brachial valve ; dorsal pallial sinus pattern digitate.

|            |                                                | length | width (mm.) |
|------------|------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of pedicle valve<br>(BB.29003)  | 12.5   | —           |
| PARATYPES. | Internal mould of pedicle valve<br>(BB.29004)  | 15.5   | —           |
|            | External mould of brachial valve<br>(BB.29005) | 9.5    | 16.5        |
|            | Internal mould of brachial valve<br>(BB.29006) | 12.5   | —           |
|            | External mould of brachial valve<br>(BB.29007) | 11.0   | 16.5        |

HORIZON AND LOCALITIES. Gelli-grŷn Group: Holotype, BB.29003 from calcareous ashes above the limestone in the old quarries and BB.29005-07 from calcareous ash crags 75 ft. south-east of deserted buildings in Ffridd Bach, south of Maesmeillion ; BB.29004 from ashy mudstones exposed on the right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern.

DISCUSSION. Representatives of the genus *Nicolella* are known to occur sporadically throughout the Upper Ordovician rocks of Britain and are probably remnants of a number of independent stocks although at present it is customary to identify them all as being closely related to *N. actoniae* (J. de C. Sowerby 1839) the type species for the genus. This procedure is, to some extent, understandable in that Sowerby's brief diagnosis was based on two distinct orthaceid moulds (see Williams 1955 : 406) and no emended description has ever been published. A small



collection of moulds from Actonian sandstones exposed in the vicinity of Acton Scott, which are topotypic with the lectotype chosen by Williams (1955 : 406), has been used to provide a revised account of the species and it is clear that specimens of *Nicolella* found in the Gelli-grin beds of the Bala district belong to a closely related group meriting only sub-specific recognition.

TABLE 2

|                                       |     | A                | B                |
|---------------------------------------|-----|------------------|------------------|
| $\bar{l}$ mm. (var. l)                | . . | 5.4 (8.668)      | 12.5 (38.062)    |
| $\bar{w}$ mm. (var. w)                | . . | 9.0 (18.548)     | 18.7 (64.986)    |
| r                                     | . . | 0.989            | 0.978            |
| $^1\log_e \bar{l}$ (var. $\log_e l$ ) | . . | 1.563 (0.2578)   | 2.4185 (0.2175)  |
| $\log_e \bar{w}$ (var. $\log_e w$ )   | . . | 2.0952 (0.2061)  | 2.84 (0.1716)    |
| $r_e$                                 | . . | 0.989            | 0.968            |
| $\alpha$ (var. $\alpha$ )             | . . | 0.8942 (0.00031) | 0.8883 (0.00207) |

TABLE 2. Statistics of length (l) and maximum width (w) of 59 brachial valves of *Nicolella actoniae obesa* subsp. nov. (A) and of 26 brachial valves of *Nicolella actoniae* (J. de C. Sowerby) (B).

TABLE 3

|                          |     | A                | B                |
|--------------------------|-----|------------------|------------------|
| $\bar{l}$ mm. (var. l)   | . . | 8.95 (11.804)    | 15.1 (20.912)    |
| $\bar{th}$ mm. (var. th) | . . | 3.7 (2.566)      | 4.6 (1.928)      |
| r                        | . . | 0.843            | 0.988            |
| a (var. a)               | . . | 0.4662 (0.00483) | 0.3036 (0.00011) |

TABLE 3. Statistics of length (l) and maximum depth (th) of 15 pedicle valves of *Nicolella actoniae obesa* subsp. nov. (A) and of 22 pedicle valves of *Nicolella actoniae* (J. de C. Sowerby) (B).

TABLE 4

|                          |     |                  |
|--------------------------|-----|------------------|
| $\bar{l}$ mm. (var. l)   | . . | 16.4 (13.524)    |
| $\bar{sc}$ mm. (var. sc) | . . | 6.8 (3.694)      |
| r                        | . . | 0.981            |
| a (var. a)               | . . | 0.5226 (0.00103) |

TABLE 4. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 12 specimens of *Nicolella actoniae* (J. de C. Sowerby).

TABLE 5

|                        |     | A               | B                |
|------------------------|-----|-----------------|------------------|
| $\bar{l}$ mm. (var. l) | . . | 4.9 (1.231)     | 7.3 (1.335)      |
| $\bar{w}$ mm. (var. w) | . . | 4.4 (0.686)     | 6.6 (0.967)      |
| r                      | . . | 0.785           | 0.956            |
| a (var. a)             | . . | 0.7465 (0.3315) | 0.8511 (0.00623) |

TABLE 5. Statistics of length (l) and maximum width (w) of ventral muscle scars of eight pedicle valves of *Nicolella actoniae obesa* subsp. nov. (A) and of twelve pedicle valves of *Nicolella actoniae* (J. de C. Sowerby) (B).

<sup>1</sup>  $\log_e \bar{l}$  (and all similarly styled terms) is an approximation to  $\overline{\log_e l}$  derived in the manner suggested by Kermack & Haldane (1950)—see Williams 1962 : 72.



In outline and profile the Bala and Acton Scott samples are very much alike. Both tend to be widest at the hinge-line and commonly attain a mucronate condition and although the Acton Scott moulds are relatively longer, comparisons of their growth rates and indices of inherent shape (Table 2) show that this difference is not important. The pedicle valves of both samples were evenly convex in lateral and longitudinal profiles but those from Bala were consistently deeper relative to length and a comparison of growth rates (Table 3) shows that their depth increased at a significantly faster rate than those from Acton Scott ( $p < .02$ ).

Shells from both lots were ornamented by sporadically occurring concentric lamellae and also by strong, angular costae with a mean wavelength (with variance) 5 mm. antero-medially of the dorsal umbones, of 1.05 mm. (0.023) and 1.03 (0.079) in 15 and 27 brachial valves of *N. actoniae* and the new subspecies respectively. The basic pattern in both samples consisted of 5 costae on either side of the median plane to the brachial valve with primary 1 apparently arising very early from primary 2 just anterior of the protogulum which was about 0.3 mm. long. These 10 costae occupied a sector of approximately  $120^\circ$  about the median line and during subsequent growth of the shell new costae arose within the wide postero-lateral sectors. Thus at the 7.5 mm. growth stage 11, 12, 13, 14 and 15 primaries were counted in 1, 1, 3, 2 and 2 brachial valves of *N. actoniae* compared with 6, 11, 9, 7 and 0 brachial valves of *N. actoniae obesa*. Within this growth stage, too, 3 out of 10 brachial valves belonging to the Acton Scott sample had developed secondary costellae branching internally from one or more of the 10 primary costae with secondary 3a arising before 1a in two out of three specimens in the former sample and in eight out of fourteen specimens in the latter. The Bala shells therefore tend to have fewer costae but more costellae in early stages of growth but the differences are not important.

The few data available for a comparison of internal morphology show that in this respect too, the samples are similar. The suboval ventral muscle fields in three pedicle valves of the new subspecies were, on an average, two-fifths as long as the valves and are indistinguishable in relative length from those of *N. actoniae* (Table 4); while comparisons of the growth rates and indices of inherent shape for their outlines (Table 5) show no important difference. It is, however, noteworthy that Bala shells attaining a dorsal length of about 12 mm. were excessively thick due to heavy secretion of secondary shell substance so that the intersetal eminences (see Williams & Wright 1963: 19) stood high above the internal margins of the valves. A comparable condition was found in the Acton Scott sample only in shells in excess of 18 mm. long which suggests that such adults grew faster and attained an absolutely greater size.

In review then it can be said that the two samples are closely related morphologically. None the less the Bala shells were significantly deeper in their ventral profiles and were also probably smaller in absolute size and in recognition of these differences the new subspecies is proposed.



## Family DOLERORTHIDAE Öpik 1934

Genus **DOLERORTHIS** Schuchert & Cooper 1931

TYPE SPECIES. *Orthis interplicata* Foerste by original designation of Schuchert & Cooper (1931 : 88).

***Dolerorthis duftonensis*** (Reed) ***prolixa*** subsp. nov.  
(Pl. 2, figs. 6, 8-13)

DIAGNOSIS. Subquadrate unequally biconvex *Dolerorthis* with rectangular or slightly obtuse cardinal angles, brachial valve about three-quarters as long as wide, gently sulcate medianly but evenly convex in longitudinal and lateral profiles, less than one-fifth as deep as long, dorsal interarea anacline, strongly developed, about one-eighth as long as valve, notothyrium open ; pedicle valve highly convex over one-quarter as deep as long, triangular in longitudinal profile with long apsacline interarea, delthyrium open but very narrow to slit-like ; ornamentation finely costellate, cancellated by fine concentric lamellae at about 7 per mm. 5 mm. anterior of dorsal umbo, with 2 costellae per mm. at about 10 mm. antero-medianly of dorsal umbo, costellae evenly rounded in transverse profile with parallel sides, arising by lateral branching from 10 to 14 primaries and including internal secondaries originating almost invariably within 5 mm. of dorsal umbo in second, third, fourth and fifth sectors so that 3â was commonly earliest and 2â the latest ; teeth strong, dental lamellae slightly divergent, strong extending anteriorly of umbo above floor of valve for about one-fifth the length of valve, muscle scar extending anteriorly for about one-third the length of pedicle valve, initially cordate in outline and about as wide as long but later extended anteriorly to become subrhomboidal, although lanceolate median adductor scar never completely surrounded by diductor sub-median lobes ; ventral pallial sinus pattern saccate with contiguous *vascula media* ; cardinal process simple, blade-like, sporadically flanked in adult brachial valves by pair of low ridges on notothyrial floor, brachiophores simple, rod-like with their bases extending anteriorly of dorsal umbo for less than one-fifth the length of valve and about one-half as long as wide, dorsal adductor muscle field quadripartite extending anteriorly of umbo for over one-half the length of brachial valve, posterior scars larger than anterior, median ridge low, dorsal pallial sinus pattern apocapate.

|            |                                                              | length | width (mm.) |
|------------|--------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal and external moulds of brachial valve (BB.29008-09) | 12.0   | 14.0        |
| PARATYPES. | Internal mould of brachial valve (BB.29010)                  | 19.5   | 23.0        |
|            | Internal mould of pedicle valve (BB.29011)                   | 16.0   | 17.5        |
|            | External mould of pedicle valve (BB.29012)                   | —      | —           |
|            | External mould of brachial valve (BB.29013)                  | —      | 21.5        |
|            | Internal mould of pedicle valve (BB.29014)                   | 27.0   | 29.0        |



HORIZON AND LOCALITIES. Gelli-grîn Group : BB.29008-09 from calcareous ashes exposed on the northern flank of the southernmost outlier of Rhiwlas rocks on Creigiau Bychain about 500 yds. north-east of Glyn-bach ; BB.29011 and 29013 from calcareous ashes above limestone exposed in quarries east of fence and 650 ft. west-north-west of BM.1407.6, south side of Bryn-Pig ; BB.29010 and 29014 from calcareous ashes above limestone in old quarry, 1,100 ft. west-south-west of Gelli-grîn Farm ; BB.29012 from ashy mudstones forming crags 1,600 ft. south-south-east of Bryn-bedwog Farm.

DISCUSSION. *Dolerorthis* is fairly common in the Gelli-grîn Group and sufficiently good collections were made to provide data for a number of attributes (see Tables 6 to 15). The stock is clearly related to *Dolerorthis duftonensis* (Reed 1910 : 295) but a comparative study of a small sample of topotypic *D. duftonensis* from Upper Longvillian mudstones exposed on the Alston Road, north-east of Melmerby (Loc. H of Dean 1959 : 210) shows that the north Welsh shells were different enough to warrant taxonomic recognition.

In the brachial valves despite an overall likeness, three distinct differences can be demonstrated. The Welsh *Dolerorthis*, are, on an average, three-quarters as long as wide, a proportion that did not greatly change during growth (Table 6). Five brachial valves of *D. duftonensis*, varying in length from 9.4 to 23.5 mm. had a mean percentage length relative to width of 82.3 (variance 45.128) and a Rank Sum test shows that they are significantly longer ( $p < .05$ ). The average percentage depth relative to length of seven brachial valves of *D. duftonensis* was 17.3 (variance 13.015), very like that for the new subspecies (Table 7) as were also the relative length of the dorsal adductor scars (Table 11) and the relative extension of the brachiophore bases anterior of the dorsal umbo (Table 9). But comparisons of relative growth rates governing the anterior extension of the dorsal interareas (Table 8) and the lateral extension of the brachiophore bases (Table 10) show that they had been significantly faster ( $p < .001$  and  $p < .05$  respectively) in the new subspecies.

A few differences have also been observed in the morphology of the pedicle valve. Three valves of *D. duftonensis* 12, 11 and 13.5 mm. long, had a relative percentage thickness of 37.5, 50.0 and 44.4 compared with an average of only 29 for the Welsh valves (Table 12). In both stocks the ventral muscle field tend to be cordate and about as long as wide during early growth stages. The anterior extension of the entire scar was, however, greatly and comparably accelerated relative to its width in adult valves (Table 15), but not relative to the length of the valves. Thus in five pedicle valves, ranging in length from 10.5 to 17.0 mm., the mean percentage length of scars relative to valves was 26.6 (variance 3.61) ; a Rank Sum test showed that these relative lengths were significantly less ( $p = .028$ ) than those for the new subspecies (Table 14). The anterior extension of the dental lamellae relative to the valve length is also less in *D. duftonensis* with a mean percentage (and variance) of 17.7 (2.49) in five valves, but the difference was not important.

The radial ornamentation of this group of *Dolerorthis* is quite distinctive. In the new subspecies, costellae arose by lateral branching from 10, 11, 12, 13 and 14



primary costae in 2, 8, 3, 2 and 1 brachial valves respectively and were sufficiently fine to number 1 and 2 per mm. in 1 and 7 brachial valves respectively at 10 mm. anterior of the umbones. Secondary internal branching took place quite early during growth. Thus within 5 mm. of the umbones of 20 brachial valves, 1ā, 2ā, 3ā, 4ā, 5ā and 6ā occurred in 10, 19, 20, 19 and 15 valves respectively. In contrast external branching within the same growth stages of the same valves was rare for 2a°, 3a°, 4a° and 5a° appeared in only 2, 4, 5 and 4 valves respectively. The relative occurrence of the internal costellae may be summarised in the following manner: 3ā appears before 4ā in 14 out of 20 valves, 4ā before 5ā in 15 out of 20 valves (in two valves they arose at about the same growth stage) and 5ā before 2ā in 15 out of 20 valves. These patterns are consistent with those observed on a few brachial valves of *D. duftonensis*.

In summary then, *D. duftonensis proluxa* differs from *D. duftonensis*, in its relatively longer brachial valve and dorsal interarea, in the lateral spread of its brachioophores, in its shallower pedicle valve and in its relatively longer ventral muscle field. Both stocks also bear some resemblance to *D. tenuicosta* (Williams 1955: 406) but can immediately be distinguished, amongst other features, by the relative coarseness of their radial ornamentation.

TABLE 6

|                        |   |   |                 |
|------------------------|---|---|-----------------|
| $\bar{l}$ mm. (var. l) | . | . | 11.2 (29.189)   |
| $\bar{w}$ mm. (var. w) | . | . | 14.9 (45.799)   |
| r                      | . | . | 0.981           |
| a (var. a)             | . | . | 1.253 (0.00281) |

TABLE 6. Statistics of length (l) and maximum width (w) of 23 brachial valves of *Dolerorthis duftonensis proluxa* subsp. nov.

TABLE 7

|                                       |   |   |                 |
|---------------------------------------|---|---|-----------------|
| $\bar{l}$ mm. (var. l)                | . | . | 11.5 (22.836)   |
| $\bar{th}$ mm. (var. th)              | . | . | 2.0 (1.221)     |
| r                                     | . | . | 0.718           |
| $\log_e \bar{l}$ (var. $\log_e l$ )   | . | . | 2.3613 (0.1605) |
| $\log_e \bar{th}$ (var. $\log_e th$ ) | . | . | 0.5349 (0.2759) |
| $r_e$                                 | . | . | 0.742           |
| $\alpha$ (var. $\alpha$ )             | . | . | 1.311 (0.02665) |

TABLE 7. Statistics of length (l) and thickness (th) of 31 brachial valves of *Dolerorthis duftonensis proluxa* subsp. nov.



TABLE 8

|                                            | A               | B               |
|--------------------------------------------|-----------------|-----------------|
| $\bar{l}$ mm. (var. l) . . .               | 13.4 (18.328)   | 12.4 (39.32)    |
| $\bar{m}$ mm. (var. in) . . .              | 1.6 (0.343)     | 1.3 (0.32)      |
| r . . .                                    | 0.858 . . .     | 0.972           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . .  | 2.5498 (0.0970) | 2.4037 (0.2279) |
| $\log_e \bar{m}$ (var. $\log_e in$ ) . . . | 0.4208 (0.1231) | 0.1391 (0.1839) |
| $r_e$ . . .                                | 0.867 . . .     | 0.983           |
| a (var. a) . . .                           | 0.137 (0.00013) | 0.092 (0.00005) |

TABLE 8. Statistics of length of brachial valve (l) and length of dorsal interarea (in) for 41 specimens of *Dolerorthis duftonensis proluxa* subsp. nov. (A) and for 11 specimens of *D. duftonensis* (Reed) (B).

TABLE 9

|                                 | A                | B               |
|---------------------------------|------------------|-----------------|
| $\bar{l}$ mm. (var. l) . . .    | 13.1 (17.96)     | 12.4 (39.32)    |
| $\bar{c}$ mm. (var. c) . . .    | 2.4 (0.505)      | 2.1 (1.204)     |
| r . . .                         | 0.932 . . .      | 0.97            |
| $\alpha$ (var. $\alpha$ ) . . . | 0.1677 (0.00011) | 0.1749 (0.0002) |

TABLE 9. Statistics of length of brachial valve (l) and length of cardinalia bases (c) for 39 specimens of *Dolerorthis duftonensis proluxa* subsp. nov. (A) and for 11 specimens of *D. duftonensis* (B).

TABLE 10

|                              | A               | B              |
|------------------------------|-----------------|----------------|
| $\bar{l}$ mm. (var. l) . . . | 2.4 (0.586)     | 2.1 (1.204)    |
| $\bar{w}$ mm. (var. w) . . . | 4.9 (1.912)     | 3.5 (2.563)    |
| r . . .                      | 0.884 . . .     | 0.972          |
| a (var. a) . . .             | 1.807 (0.02161) | 1.459 (0.0134) |

TABLE 10. Statistics of length (l) and maximum width (w) of the cardinalia bases for 35 brachial valves of *Dolerorthis duftonensis proluxa* subsp. nov. (A) and for 11 brachial valves of *D. duftonensis* (Reed) (B).

TABLE 11

|                                             | A                | B                |
|---------------------------------------------|------------------|------------------|
| $\bar{l}$ mm. (var. l) . . .                | 14.4 (21.295)    | 13.4 (38.79)     |
| $\bar{sc}$ mm. (var. sc) . . .              | 7.9 (4.729)      | 7.0 (9.8)        |
| r . . .                                     | 0.966 . . .      | 0.987            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . .   | 2.6208 (0.097)   | 2.4995 (0.1946)  |
| $\log_e \bar{sc}$ (var. $\log_e sc$ ) . . . | 2.0246 (0.0744)  | 1.8579 (0.1818)  |
| $r_e$ . . .                                 | 0.985 . . .      | 0.99             |
| $\alpha$ (var. $\alpha$ ) . . .             | 0.8758 (0.00176) | 0.9665 (0.00232) |

TABLE 11. Statistics of length of brachial valve (l) and extension of adductor scars anterior of the umbo (sc) of 15 specimens of *Dolerorthis duftonensis proluxa* subsp. nov. (A) and of 10 specimens of *D. duftonensis* (Reed) (B).



TABLE 12

|                          |   |   |        |           |
|--------------------------|---|---|--------|-----------|
| $\bar{l}$ mm. (var. l)   | . | . | 14.7   | (18.221)  |
| $\bar{th}$ mm. (var. th) | . | . | 4.2    | (1.81)    |
| r                        | . | . | 0.67   |           |
| a (var. a)               | . | . | 0.3152 | (0.00209) |

TABLE 12. Statistics of length (l) and maximum depth (th) of 29 pedicle valves of *Dolerorthis duftonensis proluxa* subsp. nov.

TABLE 13

|                          |   |   |        |           |
|--------------------------|---|---|--------|-----------|
| $\bar{l}$ mm. (var. l)   | . | . | 17.9   | (24.924)  |
| $\bar{dl}$ mm. (var. dl) | . | . | 3.7    | (1.739)   |
| r                        | . | . | 0.761  |           |
| a (var. a)               | . | . | 0.2642 | (0.00244) |

TABLE 13. Statistics of length of pedicle valve (l) and anterior extension of dental lamellae (dl) of 14 specimens of *Dolerorthis duftonensis proluxa* subsp. nov.

TABLE 14

|                                       |   |   |        |           |
|---------------------------------------|---|---|--------|-----------|
| $\bar{l}$ mm. (var. l)                | . | . | 14.8   | (14.14)   |
| $\bar{sc}$ mm. (var. sc)              | . | . | 5.0    | (2.835)   |
| r                                     | . | . | 0.762  |           |
| $\log_e \bar{l}$ (var. $\log_e l$ )   | . | . | 2.6651 | (0.0631)  |
| $\log_e \bar{sc}$ (var. $\log_e sc$ ) | . | . | 1.5514 | (0.1079)  |
| $r_e$                                 | . | . | 0.765  |           |
| $\alpha$ (var. $\alpha$ )             | . | . | 1.308  | (0.01867) |

TABLE 14. Statistics of length of pedicle valve (l) and length of ventral muscle field (sc) of 40 specimens of *Dolerorthis duftonensis proluxa* subsp. nov.

TABLE 15

|                                     |   |   |        |           |
|-------------------------------------|---|---|--------|-----------|
| $\bar{l}$ mm. (var. l)              | . | . | 5.0    | (2.607)   |
| $\bar{w}$ mm. (var. w)              | . | . | 4.0    | (1.067)   |
| r                                   | . | . | 0.896  |           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | . | 1.5615 | (0.0997)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) | . | . | 1.3402 | (0.0669)  |
| $r_e$                               | . | . | 0.9342 |           |
| $\alpha$ (var. $\alpha$ )           | . | . | 0.8191 | (0.00329) |

TABLE 15. Statistics of length (l) and maximum width (w) of the ventral muscle field of 28 specimens of *Dolerorthis duftonensis proluxa* subsp. nov.***Dolerorthis* sp.**

(Pl. 2, figs. 14-16 ; Text-fig. 7)

| MATERIAL (Figured).                                            | length | width (mm.) |
|----------------------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.29152)                  | 11.5   | 12.5        |
| Incomplete internal mould of<br>brachial valve (BB.29153)      | 7.0    | —           |
| Fragment of external mould of<br>brachial (?) valve (BB.29154) | —      | —           |



**HORIZON AND LOCALITY.** Allt Ddu Group : all specimens from sandstone and siltstone exposures about 80 ft. north of the gutter on Craig y Gath (type locality of *Howellites ultima* Bancroft 1945 : 209).

**DISCUSSION.** *Dolerorthis duftonensis* (Reed) *prolixa* subsp. nov. first occurs just above the Pont-y-Ceunant Ash and is common throughout the succeeding ashes and limestones of the Gelli-grîn Group. A few specimens belonging to the genus have also been recovered from one exposure of the highest Allt Ddu sandstones and siltstones and at first sight appear to be quite distinct from the new subspecies. In terms of shape and outline the differences are not important for the faintly sulcate brachial valve is slightly less than four-fifths as long as wide and over one-quarter as deep as long compared with a relative depth of about one-third for the pedicle valve. A fragment of what is probably the external mould of a brachial valve shows that the radial ornamentation was probably costate but the entire mould could not have been more than 8 mm. long and this condition could have been related to the small size of the valve. The moulds, however, are not the remains of young shells because the pallial sinus patterns are beautifully preserved for both valves. These impressions are usually found in only mature adult or gerontic specimens and they are not seen in the interiors of *D. duftonensis prolixa* until the shells are about twice the size of those from the Allt Ddu beds. In other words the specimens being described grew at about one-half the rate of their younger relatives but whether this difference reflects a genetic change or simply an unfavourable environment prior to the deposition of the calcareous ashes, when many of the Gelli-grîn brachiopod species tended to be larger than average, remains to be seen.

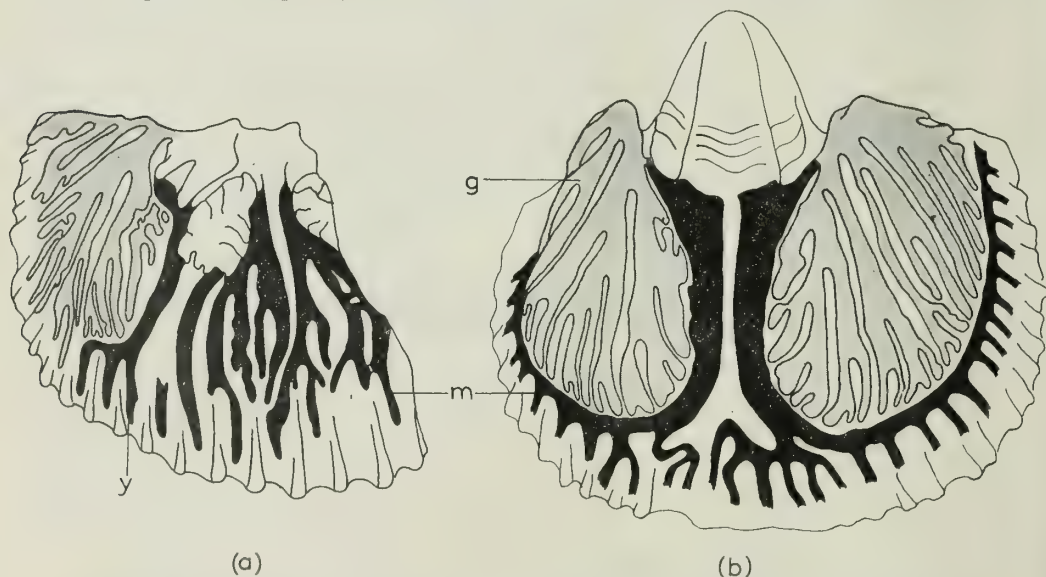


FIG. 7. The dorsal (a) and ventral (b) internal moulds of *Dolerorthis* sp.,  $\times 6.0$  approx., showing the pallial sinus patterns : g, impression of gonocoele ; m, *vascula media* ; y, *vascula myaria*.



The most interesting aspect of the pallial sinus impressions (Text-fig. 7) is the abbreviation of the posterolateral arcs of the *vascula media* in the pedicle valve and the existence of *vascula myaria* in the brachial valve. These features suggest that the ventral saccate condition and the dorsal apocopate pattern of later *Dolerorthis* (Öpik 1934 : 56 ; Williams 1956 : 278) were secondarily derived.

Family DINORTHIDAE Schuchert & Cooper 1931

Genus **DINORTHIS** Hall & Clarke 1892

TYPE SPECIES. *Orthis pectinella* Emmons by original designation of Hall & Clarke (1892 : 195).

***Dinorthis flabellulum*** (J. de C. Sowerby)

(Pl. 3, figs. 1-4)

1839 *Orthis flabellulum* J. de C. Sowerby : 639, pl. 21, fig. 8, *non* pl. 19, fig. 8.

DIAGNOSIS (emended). Subquadrate, convexo-plane to gently concave *Dinorthis* with evenly convex brachial valve almost one-quarter as deep as long and pedicle valve, less than three-quarters as long as wide, essentially planar in profile but with raised umbo and margins commonly gently deflected ventrally to give gently concave disposition ; ventral interarea apsacline, dorsal interarea commonly orthocline, up to one-tenth as long as brachial valve ; radial ornamentation consisting of strong costae with wavelength of almost 0.8 mm., 5 mm. antero-medianly of ventral umbo, and commonly numbering 24 to 26 in pedicle valves over 10 mm. long ; ventral muscle scar elongately subrectangular, extending anteriorly for almost one-half the length of pedicle valve and about four-fifths as wide as long, teeth small, dental lamellae divergent, short, less than one-tenth as long as pedicle valve ; cardinal process fully differentiated into shaft and expanded, crenulated myophore in about one-half of brachial valves between 12 and 20 mm. long, brachioophores simple and unsupported, suboval in section and extending forward of dorsal umbo at their junction with valve floor for about one-sixth the length of brachial valve, and for less than two-thirds the lateral extension of simple sockets ; dorsal adductor field, suboval and extending anterior of dorsal umbo for over one-half the length of brachial valve but rarely impressed on either side of short, low median ridge.

MATERIAL (Figured).

|                                                | length | width (mm.) |
|------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.28934)  | 24.1   | 26.8        |
| Internal mould of brachial valve<br>(BB.29023) | 20.0   | 27.9        |
| External mould of pedicle valve<br>(BB.28935)  | 19.2   | 28.3        |
| External mould of brachial valve<br>(BB.29024) | 20.8   | 27.5        |

HORIZON AND LOCALITY. Costonian Stage : all specimens from yellow weathering sandstones exposed in the vicinity of Coston Farm, one mile east-south-east of Clunbury.



*Dinorthis berwynensis* (Whittington)

(Pl. 3, figs. 5, 6, 9, 10)

1938 *Orthis calligramma* var *berwynensis* Whittington : 243, pl. 10, figs. 1-3.

DIAGNOSIS (emended). Subquadrate, convexo-plane to gently concave *Dinorthis* with brachial valve over one-quarter as deep as long, tending to be more strongly convex medianly and pedicle valve, less than three-quarters as long as wide, essentially planar in transverse profile but with raised umbo, and shallow sulcus, originating at about 6 mm. anterior of umbo and embracing about 6 costae, together imparting slight concavity to longitudinal profile ; ventral interarea apsacline, dorsal interarea commonly orthocline about one-twelfth as long as brachial valve ; radial ornamentation in pedicle valves over 5 mm. long, costate and consisting of 21 to 26 costae with wavelength of nearly 0.5 mm., 5 mm. antero-medianly of ventral umbo ; teeth small, dental lamellae, divergent, short, about one-seventh the length of pedicle valve, subrectangular ventral muscle scar over nine-tenths as wide as long and extending anterior of ventral umbo for less than two-fifths the length of pedicle valve ; cardinal process commonly fully differentiated into shaft and expanded, crenulated myophore in brachial valves over 8.0 mm. long, brachiophores simple and unsupported, suboval in cross section and extending forward of dorsal umbo at their junction with valve floor for over one-sixth the length of brachial valve and for over one-half lateral extension of simple sockets, dorsal adductor field suboval and extending forward of umbo for about one-half the length of brachial valve but rarely impressed on either side of short, low median ridge.

## MATERIAL (Figured).

|                                                | length | width (mm.) |
|------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.28982)  | 6.3    | 8.4         |
| Internal mould of brachial valve<br>(BB.28983) | —      | —           |
| External mould of pedicle valve<br>(BB.28984)  | 11.9   | —           |
| Internal mould of brachial valve<br>(BB.29025) | 3.8    | —           |

HORIZONS AND LOCALITIES. Glyn Gower Group : BB.28982 from siltstones exposed between parallel paths on the west side of Y Foel, 1,300 ft. south-south-east of Coed-y-foel-uchaf Farm ; BB.28983-84 from siltstone crags in wood immediately east of Cefn-bodig Farm. Lower Allt Ddu Group : BB.29025 from siltstones immediately above the Fron-dderw Ash and about 600 ft. north of Fron-dderw Farm.

*Dinorthis berwynensis* (Whittington) *angusta* subsp. nov.

(Pl. 3, figs. 7, 8, 11-14)

DIAGNOSIS. Subquadrate, convexo-plane to gently concave *Dinorthis* with brachial valve nearly two-fifths as deep as long, tending to be more strongly convex medianly and pedicle valve less than four-fifths as long as wide, essentially planar



in transverse profile but with raised umbo and shallow sulcus, originating at about 6 mm. anterior of umbo and embracing 7 or 8 costae, together imparting a slight concavity to the longitudinal profile ; ventral interarea apsacline, dorsal interarea commonly orthocline, about one-twelfth as long as brachial valve ; radial ornamentation costate and, in pedicle valves over 5 mm. long, consisting of 21 to 26 costae with wavelength of over 0.4 mm., 5 mm. antero-medially of ventral umbo ; teeth small, dental lamellae divergent, short, about one-sixth as long as pedicle valve, subrectangular ventral muscle scar less than nine-tenths as wide as long and extending forward of umbo for less than two-fifths the length of pedicle valve ; cardinal process fully differentiated into shaft and expanded, crenulated myophore in valves more than 6 mm. long, brachioophores simple and unsupported, suboval in cross section and extending forward of dorsal umbo at their junction with valve floor for over one-fifth the length of brachial valve and for over one-half the lateral extension of simple sockets, dorsal adductor field suboval and extending forward of umbo for about one-half the length of brachial valve but rarely impressed on either side of short, low median ridge.

|            |                                                              | length | width (mm.) |
|------------|--------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal and external moulds of pedicle valves (BB.28978-79) | 14.3   | 19.6        |
| PARATYPES. | Internal and external moulds of pedicle valve (BB.28980-81)  | 11.0   | —           |
|            | Internal mould of brachial valve (BB.29026)                  | 6.7    | 7.1         |
|            | Internal mould of brachial valve (BB.29027)                  | 12.0   | —           |

**HORIZON AND LOCALITY.** Allt Ddu Group : all specimens from fine sandstones and mudstones immediately below the Pont-y-Ceunant Ash and exposed in crags north of the drive to Y Garnedd.

**DISCUSSION.** *Dinorthis* is known to occur in the upper part of the Glyn Gower Group as well as in the Allt Ddu Group, but examples are common only in the strata succeeding the Fron-dderw Ash, where they are associated with *Heterorthis retrorsistria*, and again in the sandy beds immediately underlying the Gelli-grŷn Group. The radial ornamentation of the specimens recovered is almost invariably costate which immediately separates them from the Costonian and Soudleyan species of *Plaesiomys* described by Bancroft (1945 : 240-245) and suggests affinities with the similarly ornamented *Dinorthis flabellulum* (J. de C. Sowerby) and *D. berwynensis* (Whittington). The older stock is indistinguishable in every aspect of its morphology from the latter species, and a sample taken from siltstones just below and above the Fron-dderw Ash has been used to provide an emended diagnosis of *D. berwynensis*. The high Allt Ddu forms differed significantly from both species but is much more removed from *D. flabellulum* and, in order to recognise this disparity, it has been described as a new subspecies *D. berwynensis angusta*.



The sample of *D. flabellulum* was not entirely satisfactory in that it consisted mainly of mature shells, commonly up to three times as large as those in the collections from Bala, and this is probably reflected in the number of costae ornamenting the pedicle valves (Table 22). The differences are not important, but, as can be seen, larger shells tend to have more costae which arose in the postero-lateral areas well away from the umbo, so that the higher modal value for *D. flabellulum* is to be expected. This would also explain the apparent anomaly of the broader costae of *D. flabellulum*. At a distance of 5 mm. antero-medially of the ventral umbo the mean wavelength (with variance) of the costae of 23 specimens of *D. flabellulum* was 0.77 (0.033) compared with 0.48 (0.003) for 16 specimens of *D. berwynensis* and 0.44 (0.006) for 17 specimens of the new subspecies. In all three samples, the costae are smoothly rounded in transverse profile but those of *D. flabellulum* are significantly wider ( $p < .001$ ) than those ornamenting the Bala specimens. With respect to the influence of size on the pattern of ornamentation, one other fact is noteworthy. In the largest pedicle valve of *D. berwynensis*, which at 14 mm. in length is still smaller than the average length of the *D. flabellulum* valves, secondary costellae branch off from 5 costae near the margin; and two secondaries also occur in each of two valves of the new subspecies, 6.5 and 8 mm. long respectively. This earlier occurrence of costellation in the sample is still exceptional in that it was found in only 2 out of 24 valves over 6.5 mm. long; but the possibility remains that had the Bala shells attained the size of the *D. flabellulum* ones, a late costellate condition might have been more characteristic of them than a costate one.

Statistics assessing the relative growth of a number of morphological features in all three samples are given in Tables 16-21, 23, 24. Apart from the outline and relative length of its cardinalia, for which the derived coefficients of correlation ( $r$ ) are not significant, *D. flabellulum* can be shown to differ importantly from the Bala shells in many ways. Thus, although all three stocks increased in the relative depth of their brachial valves at about the same rates, the inherent convexity ( $\beta$ ) of *D. flabellulum* was significantly greater than that of the others ( $p < .001$ ). Similarly, the ventral muscle field of *D. flabellulum* extended anteriorly at a significantly faster rate ( $p < .01$ ) than that of the Bala *Dinorthis* (Table 17) but at the same time retained a subrectangular outline comparable, both in growth and residual proportions, with the other two (Table 18). The dental lamellae of both Bala samples also proved to be significantly longer ( $.05 > p > .02$ ) than those of *D. flabellulum* although for different reasons, because those of *D. berwynensis* grew at about the same rate but were inherently longer whereas those of the new subspecies extended anteriorly much more quickly relative to the increase in valve length. Finally, in the outline of the pedicle valve (Table 21) *D. flabellulum* is close to *D. berwynensis* in that both of them are inherently wider relative to length than *D. berwynensis angusta* ( $p < .001$ ). In contrast, a shallow sulcus, embracing between 5 and 9 costae antero-medially, originated at a mean distance (with variance) of 5.8 mm. (0.44) and 6.1 mm. (0.821) anterior of the umbones of 8 and 24 pedicle valves of *D. berwynensis* and *D. berwynensis angusta* respectively. The difference is not significant and since no comparable feature was observed in *D. flabellulum*



it can at least be held that the pedicle valve of *D. berwynensis* in its total external morphology is intermediate between the other two samples. Except for the difference in ventral outline referred to above, the tables show that other distinctions between *D. berwynensis* and the new subspecies are limited to attributes of the brachial valves. A comparison of the relative growth of the dorsal interareas (Table 24) reveals that those of *D. berwynensis* extended anteriorly at a significantly slower pace than those of the new subspecies ( $0.05 > p > 0.02$ ) while the brachiophore bases of *D. berwynensis* were inherently shorter ( $0.05 > p > 0.02$ ) than those of the high Allt Ddu forms (Table 19). But in the early development of a fully differentiated cardinal process they are both quite different from *D. flabellulum*. Unfortunately, data for similar size ranges were not available, but only 5 out of 11 brachial valves of *D. flabellulum*, between 15 and 20 mm. long, bore a well developed crenulated myophore as well as a stout shaft; whereas this condition had already been attained in 8 out of 8 and 4 out of 5 brachial valves, over 8 mm. long, of *D. berwynensis angusta* and *D. berwynensis* respectively.

The costate *Dinorthis* specimens from the Bala district are therefore quite distinct from *D. flabellulum* in their narrower costae, their sulcate pedicle valves, their shallower brachial valves, their well developed cardinal processes and their relatively shorter ventral muscle scars. These differences suggest that the Welsh samples are closely related to each other and the balance of morphological features confirms that this is so. But differences also exist between them—notably in the wider pedicle valve and the shorter dorsal interarea and brachiophore bases—and are important enough to warrant the erection of a new subspecies to embrace the high Allt Ddu forms.

TABLE 16

|                  | A               | B                | C               |
|------------------|-----------------|------------------|-----------------|
| l mm. (var. l)   | 16.83 (16.693)  | 9.68 (16.401)    | 8.86 (13.28)    |
| dl mm. (var. dl) | 1.64 (0.184)    | 1.33 (0.339)     | 1.45 (0.402)    |
| r                | 0.699           | 0.936            | 0.774           |
| a (var. a)       | 0.105 (0.00082) | 0.1437 (0.00015) | 0.174 (0.00044) |

TABLE 16. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) for 9 specimens of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 19 of *D. berwynensis* (Whittington) (B) and 31 of *D. berwynensis angusta* subsp. nov. (C).

TABLE 17

|                  | A                | B                | C                |
|------------------|------------------|------------------|------------------|
| l mm. (var. l)   | 16.15 (7.821)    | 8.8 (21.442)     | 8.24 (15.258)    |
| sc mm. (var. sc) | 7.87 (3.626)     | 3.36 (3.62)      | 3.1 (2.154)      |
| r                | 0.804            | 0.905            | 0.959            |
| a (var. a)       | 0.6808 (0.00965) | 0.4109 (0.00139) | 0.3758 (0.00031) |

TABLE 17. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 19 specimens of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 24 of *D. berwynensis* (Whittington) (B) and 35 of *D. berwynensis angusta* subsp. nov. (C).



TABLE 18

|                                       | A               | B                | C                |
|---------------------------------------|-----------------|------------------|------------------|
| $\bar{l}$ mm. (var. l) .              | 8.05 (2.718)    | 3.75 (1.918)     | 3.11 (2.234)     |
| $\bar{w}$ mm. (var. w) .              | 6.46 (2.207)    | 3.45 (1.272)     | 2.68 (1.184)     |
| $r$ .                                 | 0.775           | 0.945            | 0.963            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . | 2.0651 (0.0411) | 1.2581 (0.1274)  | 1.0311 (0.207)   |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . | 1.8397 (0.0517) | 1.1877 (0.1014)  | 0.9094 (0.1528)  |
| $r_e$ .                               | 0.807           | 0.958            | 0.974            |
| $\alpha$ (var. $\alpha$ ) .           | 1.122 (0.02308) | 0.8921 (0.00595) | 0.8592 (0.00115) |

TABLE 18. Statistics of length (l) and maximum width (w) of the ventral muscle scar of 21 pedicle valves of *Dinorthis flabellulum* (A), 11 of *D. berwynensis* (Whittington) (B) and of 35 *D. berwynensis angusta* subsp. nov. (C).

TABLE 19

|                                       | A             | B               | C                |
|---------------------------------------|---------------|-----------------|------------------|
| $\bar{l}$ mm. (var. l) .              | 19.16 (9.634) | 7.86 (17.646)   | 6.22 (11.315)    |
| $\bar{c}$ mm. (var. c) .              | 3.3 (0.24)    | 1.37 (0.438)    | 1.32 (0.436)     |
| $r$ .                                 | 0.574         | 0.85            | 0.98             |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . | —             | 1.9446 (0.2517) | 1.6993 (0.257)   |
| $\log_e \bar{c}$ (var. $\log_e c$ ) . | —             | 0.2001 (0.2094) | 0.166 (0.2231)   |
| $r_e$ .                               | —             | 0.866           | 0.982            |
| $\alpha$ (var. $\alpha$ ) .           | —             | 0.9121 (0.0104) | 0.9318 (0.00103) |

TABLE 19. Statistics of length of brachial valve (l) and length of brachiophores at their bases (c) for 8 specimens of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 22 specimens of *D. berwynensis* (Whittington) (B) and 32 specimens of *D. berwynensis angusta* subsp. nov. (C).

TABLE 20

|                                       | A            | B                | C                |
|---------------------------------------|--------------|------------------|------------------|
| $\bar{l}$ mm. (var. l) .              | 3.4 (0.278)  | 1.43 (0.279)     | 1.32 (0.421)     |
| $\bar{w}$ mm. (var. w) .              | 5.43 (0.168) | 2.66 (0.725)     | 2.37 (1.283)     |
| $r$ .                                 | 0.664        | 0.97             | 0.971            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . | —            | 0.294 (0.1274)   | 0.1685 (0.2167)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . | —            | 0.9293 (0.0979)  | 0.7606 (0.2053)  |
| $r_e$ .                               | —            | 0.974            | 0.973            |
| $\alpha$ (var. $\alpha$ ) .           | —            | 0.8766 (0.00282) | 0.9733 (0.00141) |

TABLE 20. Statistics of length of brachiophores at their bases (l) and width of sockets (w) for 9 brachial valves of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 16 of *D. berwynensis* (Whittington) (B) and 28 of *D. berwynensis angusta* subsp. nov. (C).



TABLE 21

|                                       | A                | B                | C                |
|---------------------------------------|------------------|------------------|------------------|
| $\bar{l}$ mm. (var. l) .              | 17.17 (7.339)    | 5.79 (15.43)     | 6.53 (9.528)     |
| $\bar{w}$ mm. (var. w) .              | 23.77 (12.186)   | 7.93 (21.624)    | 8.33 (14.269)    |
| r .                                   | 0.811            | 0.987            | 0.979            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . | 2.8039 (0.0246)  | 1.5669 (0.3784)  | 1.7757 (0.2013)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . | 3.1576 (0.0217)  | 1.9232 (0.2949)  | 2.0267 (0.1863)  |
| $r_e$ .                               | 0.801            | 0.986            | 0.971            |
| $\alpha$ (var. $\alpha$ ) .           | 0.9392 (0.01129) | 0.8828 (0.00098) | 0.9621 (0.00113) |

TABLE 21. Statistics of length (l) and maximum width (w) of 30 pedicle valves of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 24 of *D. berwynensis* (Whittington) (B) and 49 of *D. berwynensis angusta* subsp. nov. (C)

TABLE 22

## Number of costae

|           | 18-20 | 21-23 | 24-26 |
|-----------|-------|-------|-------|
| A . . . . | 3     | 2     | 12    |
| B . . . . | 1(2)  | 2(9)  | 3(4)  |
| C . . . . | 0(0)  | 6(12) | 5(13) |

TABLE 22. The number of pedicle valves over 10 mm. long (and between 5 and 10 mm. long in brackets) of *Dinorthis flabellulum* (J. de C. Sowerby) (A), *D. berwynensis* (Whittington) (B), and *D. berwynensis angusta* subsp. nov. (C) bearing between 18 and 26 costae.

TABLE 23

|                                         | A               | B               | C               |
|-----------------------------------------|-----------------|-----------------|-----------------|
| $\bar{l}$ mm. (var. l) .                | 16.08 (12.202)  | 7.61 (10.5)     | 6.68 (10.98)    |
| $\bar{th}$ mm. (var. th) .              | 3.86 (1.78)     | 2.25 (1.236)    | 2.54 (2.544)    |
| r .                                     | 0.555           | 0.862           | 0.942           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) .   | 2.7545 (0.0459) | 1.9459 (0.1672) | 1.7891 (0.2199) |
| $\log_e \bar{th}$ (var. $\log_e th$ ) . | 1.2940 (0.1133) | 0.7017 (0.2183) | 0.7664 (0.3315) |
| $r_e$ .                                 | 0.584           | 0.871           | 0.961           |
| $\alpha$ (var. $\alpha$ ) .             | 1.571 (0.04645) | 1.143 (0.0105)  | 1.228 (0.00398) |

TABLE 23. Statistics of length (l) and depth (th) of 37 brachial valves of *Dinorthis flabellulum* (J. de C. Sowerby) (A), 32 of *D. berwynensis* (Whittington) (B) and 31 of *D. berwynensis angusta* subsp. nov. (C).

TABLE 24

|                            | A                 | B                |
|----------------------------|-------------------|------------------|
| $\bar{l}$ mm. (var. l) .   | 8.4 (17.958)      | 7.08 (9.39)      |
| $\bar{in}$ mm. (var. in) . | 0.64 (0.098)      | 0.6 (0.0544)     |
| r .                        | 0.923             | 0.916            |
| a (var. a) .               | 0.07387 (0.00005) | 0.7611 (0.00004) |

TABLE 24. Statistics of length of brachial valve (l) and length of dorsal interarea (in) for 18 specimens of *Dinorthis berwynensis* (Whittington) (A) and 24 specimens of *D. berwynensis angusta* subsp. nov. (B).



Family PLECTORTHIDAE Schuchert & Le Vene 1929

Subfamily PLATYSTROPHIINAE Schuchert & Le Vene 1929

Genus **PLATYSTROPHIA** King 1850

TYPE SPECIES. *Terebratulites biforatus* Schlotheim by original designation of King (1850 : 106).

***Platystrophia cf. sublimis*** Öpik

(Pl. 3, figs. 15-22)

DESCRIPTION. Strongly biconvex, subquadrate *Platystrophia* with the brachial valve just over two-thirds as long as wide and over one-half as deep as long, dorsal fold strong, high, less than two-thirds as wide as the valve is deep ; costae angular, covered with densely distributed pustules and numbering 2 or more commonly 3, in the ventral sulcus and 12 to 16, most commonly 15, on the flanks ; ventral interior with massive teeth, short receding dental lamellae and a subtriangular muscle field impressed on floor of the valve anterior of the umbo for just over one-third the length of the valve and just over one-half as wide as long ; cardinal process ridge-like, notothyrial platform and brachiophore supports obliterated by secondary shell deposition, adductor muscle impressions quadripartite about a low median ridge with the subtriangular anterior pair the larger.

| MATERIAL (Figured).                                            | length | width (mm.) |
|----------------------------------------------------------------|--------|-------------|
| Incomplete internal mould of<br>brachial valve (BB.29015)      | 21.0   | —           |
| Incomplete internal mould of<br>pedicle valve (BB.29016)       | 27.0   | —           |
| Incomplete external mould of<br>brachial valve (BB.29017)      | —      | —           |
| Incomplete external mould of<br>pedicle valve (BB.29018)       | —      | —           |
| Incomplete external mould of<br>pedicle valve (BB.29019)       | —      | —           |
| Incomplete external mould of<br>pedicle valve (BB.29020)       | 19.0   | —           |
| Internal and external mould of<br>brachial valve (BB.29021-22) | 5.5    | 9.5         |

HORIZON AND LOCALITIES. Gelli-grîn Group : BB.29018 from calcareous ashes exposed in the first crag on the south side of the head of the stream issuing from Craig y Gath ; other specimens from calcareous ashes cropping out immediately west of fence at south-east end of prominent Rhiwlas Limestone scarp, 500 ft. south-west of BM.1338.7, south side of Bryn Pig.

DISCUSSION. Moulds of *Platystrophia* occur sporadically in the ashes and limestones of the Gelli-grîn Group but are commonly so badly deformed that little information can be given at present on the morphological variability inherent to the stock. The pattern of radial ornamentation, however, affords some guide to the affinities of the shells and also suggests that the phylogenetic classification given



by McEwan (1920 : 383-404) requires some revision. Judging from the disposition of the costae within the ventral sulcus, the shells belong to her "biplicate (i.e. bicostate) group-subgroup A" (p. 389), in that a pair of submedian costae, presumably arising by dichotomy of a "nepionic" median costa, were characteristic of 5 ventral moulds. In 7 other moulds, however, 3 costae occupied the sulcus. In one valve the median costa is seen to have arisen by branching from the right submedian and in another the left submedian costa arose on the shoulder bounding the sulcus when the shell was a few millimetres long but during growth it became part of the floor of the sulcus; for the remaining 5 moulds it was not possible to determine the origin of the third costa. McEwan (1920 : 407) has described a species, *P. trentonensis*, that is also characterized by the presence of 3 costae in the sulcus, although in this stock, and indeed, according to McEwan (1920 : 389), in all similarly ornamented *Platystrophia* (her subgroup B), the median costa arose last and by intercalation. In effect, if the current infrageneric segregation of *Platystrophia* based on the number and mode of origin of the costae within the sulcus were adopted for the Bala shells, three species would have to be recognized within what is certainly a homogeneous sample. Unfortunately such a procedure has been general practice. Thus Öpik (1930 : 105-108) has identified specimens of *Platystrophia* from the C<sub>3α</sub> beds of Kohtla as *P. dentata* (Pander) or *P. sublimis* Öpik dependent on whether the ventral sulcus is occupied by 2 or 3 costae respectively. This association is reminiscent of the relationships within the Bala sample and although it is not yet known whether the third costa arose in a similar way, the Welsh and Baltic shells provisionally may be regarded as conspecific. It is noteworthy that in older Baltic rocks the bicostate group of *Platystrophia* is represented exclusively by the *P. dentata* type of shell because a similarly ornamented form, *P. precedens major* Williams, is recorded in the Derfel Limestone (see Whittington & Williams 1955 : 402) and in the Upper Llandeilo rocks of the Berwyn Dome (MacGregor 1961 : 184).

#### Subfamily RHACTORTHINAE nov.

Biconvex, dorsally sulcate plectorthids with hollow costellae, a subpentagonal ventral muscle field including a wide adductor scar not enclosed by the diductor lobes, a posteriorly crenulated cardinal process continuous with a dorsal median ridge and divergent brachioophore bases curving laterally to define the sockets.

#### Genus *RHACTORTHIS* nov.

DIAGNOSIS. Subquadrate, biconvex shells with deep, subcarinate pedicle valve and less convex, sharply sulcate brachial valve; radial ornamentation evenly multicostellate, broken by gross "growth lines", costellae commonly arising by dichotomy and commonly hollow; ventral interarea, straight, apsacline with wide open delthyrium, dorsal interarea short, straight, anacline, notothyrium open, occupied by posterior face of cardinal process; shell probably impunctate.

Ventral interior with massive teeth, supported by short, receding, divergent dental lamellae posteriorly enclosing subpentagonal muscle field with wide, undifferentiated adductor scar, separating narrow, divergent, submedian diductor lobes which encroach onto a pair of subparallel *vascula media*, ventral pallial sinus incompletely



known but possibly saccate with subsidiary gonadal sac anterior of muscle field, between posterior portions of *vascula media*.

Dorsal interior with ridge-like cardinal process, thickened and posteriorly crenulated in adult stages of growth but always continuous with long median ridge ; brachiophores, short, rod-like, slightly divergent and embedded in pair of bases which curve laterally away from median plane to define the sockets, adductor scars situated posteriorly on either side of median ridge, just anterior of socket ridges ; *vascula media* and *myaria* diverging and branching from adductor field possibly as part of saccate pallial sinus pattern ; interiors of both valves with strongly raised concentric ridges corresponding to external breaks in forward growth of valves.

TYPE SPECIES. *Rhactorthis crassa* sp. nov. from the Gelli-grîn Group, Bala.

DISCUSSION. The new genus, specimens of which are fairly common in the Gelli-grîn Group of the Bala district and are also known to occur in the Longvillian strata of the Welsh Borderland and the Lake District, has hitherto passed as a "dalmanellid" *s.l.* (e.g. Bancroft 1928 : 489) or an orthid *s.s.* (e.g. *Orthis melmerbiensis* Reed 1910 : 296). The arrangement of the brachiophores is admittedly like that of the dalmanellids *Bancroftina* Sinclair and *Eodalmanella* Havlíček, but fragments of shell found adherent to some of the Welsh moulds were all impunctate and as an orthaceid it is so distinctive that it can only be accommodated provisionally within a new subfamily of the Plectorthidae. There are certainly features which are also characteristic of various plectorthid genera. Dichotomous ribbing is typical of many species of *Plectorthis* Hall & Clarke ; hollow costellae were developed in *Doleroides* Cooper ; the ventral muscle field, with the wide adductor scar, is like that of *Mimella* Cooper ; and, apart from the sharp dorsal sulcus, the outline and profile of the new genus are also reminiscent of *Mimella*. The brachiophore bases of all plectorthids, however, converge on to the notothyrial platform or even the median ridge and the sockets are concomitantly defined by strong fulcral plates. By contrast, the brachiophore bases of the new genus diverge to lie more or less parallel with the hinge-line and in this attitude they not only give support to the brachiophores but also serve as confining walls to the sockets. This disposition is rare even among those dalmanellaceids with divergent brachiophore bases. It is at present unique among the orthaceids and until more is known about the development of the plectorthid cardinalia it seems best to segregate *Rhactorthis* from all other contemporary orthaceids at least at the subfamilial level.

***Rhactorthis crassa* gen. et sp. nov.**

(Pl. 4, figs. 1-6 ; Text-fig. 8)

DIAGNOSIS. Subcircular, unequally biconvex *Rhactorthis* with sulcate brachial valve, nearly three-quarters as long as wide, just over one-fifth as deep as long, and high pedicle valve nearly two-fifths as deep as long, radial ornamentation multicostellate but interrupted by thick, irregularly spaced concentric zones of negligible forward growth, costellae, commonly hollow and about 3 per mm. at a distance of 5 mm. anterior of dorsal umbo, tending to arise by dichotomous branching



with secondary externals rarely appearing in Sectors I to IV during early growth stages ; ventral muscle scar subpentagonal becoming relatively longer than wide during adult stages of growth and extending anteriorly for just over one-third the length of pedicle valve, submedian diductor lobes not projecting very much forward of wide adductor scar ; brachiophore bases widely splayed to define sockets, less than one-sixth as long as brachial valve and about two-fifths as long as wide, dorsal adductor scars elongate, extending anteriorly for about one-half of brachial valve on either side of median ridge.

|            |                                                                           | length | width (mm.) |
|------------|---------------------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of brachial valve (BB.28878)                               | 3.5    | 5.0         |
| PARATYPES. | Deformed external mould of brachial valve (BB.28879)                      | 6.5    | 10.0        |
|            | Incomplete external moulds of conjoined valves (BB.28880)                 | —      | —           |
|            | Deformed internal mould of pedicle valve (BB.24542)                       | 9.5    | 10.5        |
|            | External and internal moulds of pedicle valve (BB.28881-82)               | 8.5    | —           |
|            | Internal mould of brachial valve (BB.29028)                               | 8.5    | —           |
|            | Internal mould of pedicle valve (BB.28883)                                | 8.5    | —           |
|            | Internal mould of brachial valve (BB.28884)                               | 2.3    | 4.0         |
|            | Incomplete external mould of pedicle valve with adherent shell (BB.28885) | —      | —           |

HORIZON AND LOCALITIES. Gelli-grŷn Group : BB.28879-80, BB.29028, BB.28884 from calcareous ashes exposed on north side of the southern Rhiwlas Limestone outlier on Creigiau Bychain ; BB.28883, BB.28885 from calcareous ash outcrops on the east side of the central Rhiwlas Limestone outlier, Creigiau Bychain ; BB.28878, BB.24542 from calcareous ash crags beginning 75 ft. south of the east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28881-82 calcareous ash crags in field 600 ft. south-east of Bryn-briglas.

TABLE 25

|                                       |        |          |
|---------------------------------------|--------|----------|
| $\bar{l}$ mm. (var. $l$ ) .           | 3.9    | (3.872)  |
| $\bar{w}$ mm. (var. $w$ ) .           | 5.43   | (5.457)  |
| $r$ .                                 | 0.933  |          |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . | 1.2474 | (0.2271) |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . | 1.6069 | (0.1699) |
| $r_e$ .                               | 0.945  |          |
| $\alpha$ (var. $\alpha$ ) .           | 0.865  | (0.004)  |

TABLE 25. Statistics of length ( $l$ ) and maximum width ( $w$ ) of 22 brachial valves of *Rhactorthis crassa* gen. et sp. nov.



TABLE 26

|                          |        |           |
|--------------------------|--------|-----------|
| $\bar{l}$ mm. (var. l) . | 6.1    | (3.586)   |
| $\bar{c}$ mm. (var. c) . | 1.07   | (0.127)   |
| r .                      | 0.889  |           |
| a (var. a). .            | 0.1882 | (0.00073) |

TABLE 26. Statistics of length (l) and length of cardinalia (c) of 12 brachial valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 27

|                          |       |           |
|--------------------------|-------|-----------|
| $\bar{l}$ mm. (var. l) . | 1.08  | (0.144)   |
| $\bar{w}$ mm. (var. w) . | 2.65  | (0.547)   |
| r .                      | 0.813 |           |
| a (var. a). .            | 1.949 | (0.16103) |

TABLE 27. Statistics of length (l) and maximum width (w) of the cardinalia of 10 brachial valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 28

|                          |        |          |
|--------------------------|--------|----------|
| $\bar{l}$ mm. (var. l) . | 8.14   | (8.131)  |
| $\bar{m}$ mm. (var. m) . | 2.87   | (1.702)  |
| r .                      | 0.967  |          |
| a (var. a). .            | 0.4575 | (0.0017) |

TABLE 28. Statistics of length (l) and length of ventral muscle field (m) of 10 pedicle valves of *Rhactorthis crassa* gen. et sp. nov.

TABLE 29

|                                       |        |          |
|---------------------------------------|--------|----------|
| $\bar{l}$ mm. (var. l) .              | 3.15   | (1.565)  |
| $\bar{w}$ mm. (var. w) .              | 2.78   | (0.858)  |
| r .                                   | 0.964  |          |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . | 1.0744 | (0.1459) |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . | 0.9698 | (0.1053) |
| $r_e$ .                               | 0.964  |          |
| $\alpha$ (var. $\alpha$ ) .           | 0.8495 | (0.0051) |

TABLE 29. Statistics of length (l) and maximum width (w) of the ventral muscle field of 12 pedicle valves of *Rhactorthis crassa* gen. et sp. nov.

DISCUSSION. Most of the relevant data concerning the variability of the new species have been set out in Tables 25-29 which show that the growth of the brachial valves tended to accelerate in length relative to width in adult shells and that the ventral muscle field which was initially wider than long ultimately expanded anteriorly at a faster rate than its lateral encroachment along the valve floor. The strongly convex profiles of both valves are reflected in the mean percentage depth relative to length of 22.2 (variance 8.2) for 6 brachial valves and of 39 (range 36 to 41) for 3 pedicle valves. The radial ornamentation is rather fine with counts of 2, 3 or 4 ribs per mm. 5 mm. anterior of the dorsal umbones of 1, 5 and 1 specimens respectively. At the 2 mm. growth stage, 14-18 costae ornament the brachial valve with the secondary costellae, 1 $\bar{a}$ , 2 $\bar{a}$ , 3 $\bar{a}$ , 4 $\bar{a}$  and 4 $\bar{a}^\circ$  also appearing in 7/12, 10/12, 10/12, 2/10 and 1/10 specimens respectively. 3 $\bar{a}$  arose earlier than 1 $\bar{a}$  and 2 $\bar{a}$



in 6/8 and 5/8 specimens respectively. The dorsal adductor scars are not deeply impressed but appear to be quite variable in their percentage length measured from the umbo, relative to the length of the brachial valve which averaged 51 (range 40 to 62) in 4 internal moulds.

The only other described species known to be congeneric with *R. crassa* is *R. melmerbiensis* (Reed 1910 : 296) but although only a few specimens of this latter species were available for study they can immediately be distinguished from *R. crassa* in the strongly carinate pedicle valve which is consequently deeper with an average percentage depth relative to the length of 3 valves of 45 (range 42 to 56) and in the correspondingly deeper but wider dorsal sulcus. *R. melmerbiensis* may also ultimately prove to have a relatively wider brachial valve which is certainly more semi-oval than the new species but internally the differences appear to be negligible.

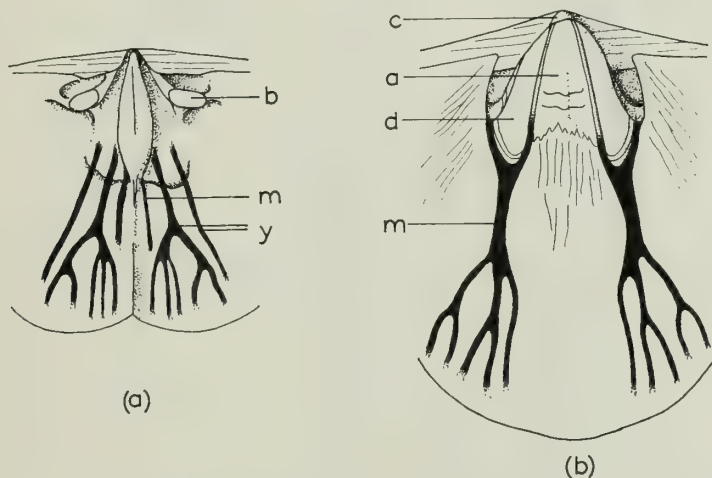


FIG. 8. The dorsal interior (a) and the ventral internal mould (b) of *Rhactorthis crassa* gen. et sp. nov.,  $\times 5$  approx.: a, adductor scar ; b, brachiophore ; c, pedicle callist ; d, diductor scar ; m, vascula media ; y, vascula myaria.

#### Family SKENIDIIDAE Kozłowski 1929

##### Genus **SKENIDIODES** Schuchert & Cooper 1931

TYPE SPECIES. *Skenidioides billingsi* Schuchert & Cooper by original designation of Schuchert & Cooper (1931 : 71).

##### ***Skenidioides cf. costatus* Cooper**

(Pl. 4, figs. 7-14)

DESCRIPTION. Semi-oval *Skenidioides* with a subpyramidal pedicle valve about three-fifths as long as wide and one-half as deep as long and a very gently convex brachial valve sharply depressed about a median sulcus ; surface essentially costate with, in the pedicle valve, a wide median costa about 0.5 mm. in wavelength 2 mm.



anterior of the umbo flanked on either side by up to 8 rounded costae with a wave-length of about 0.3 mm., costellae arising early especially in the first three sectors ; spondylium, shallow, mostly free but supported umbonally by a thickened deposit of secondary shell commonly prolonged as a ridge along the anterior surface of the spondylium and especially along the valve floor for almost one-quarter the length of the valve ; ventral pallial sinus pattern digitate ; cardinal process thin, ridge-like and continuous with the median septum which is subtriangular in outline with the apex just anterior of the mid-line, brachioophores slender, with bases convergent on to the median septum at about one-third the valve length anterior of the umbo, sockets small and defined by fulcral plates ; dorsal adductor field as a pair of lanceolate impressions divided by the septum and extending anteriorly for almost two-thirds the length of the brachial valve.

| MATERIAL (Figured).                                    | length | width (mm.) |
|--------------------------------------------------------|--------|-------------|
| Internal mould of brachial valve (BB.28917)            | 2.8    | 3.8         |
| Internal mould of pedicle valve (BB.28918)             | 4.0    | 5.5         |
| Incomplete internal mould of brachial valve (BB.28919) | —      | —           |
| Incomplete internal mould of pedicle valve (BB.28921)  | 4.7    | —           |
| Incomplete external mould of brachial valve (BB.28920) | —      | —           |
| External mould of pedicle valve (BB.28922)             | 2.3    | 4.5         |
| Deformed internal mould of brachial valve (BB.24548)   | 4.5    | 7.7         |
| Deformed internal mould of pedicle valve (BB.28924)    | 4.5    | 7.2         |

TABLE 30

|                          |                |
|--------------------------|----------------|
| $\bar{l}$ mm. (var. l) . | 2.48 (0.977)   |
| $\bar{w}$ mm. (var. w) . | 4.15 (1.536)   |
| r .                      | 0.938          |
| a (var. a) .             | 1.254 (0.0094) |

TABLE 30. Statistics of the length ( $\bar{l}$ ) and maximum width ( $\bar{w}$ ) of 22 pedicle valves of *Skenidioides* cf. *costatus* Cooper.

TABLE 31

|                            |                |
|----------------------------|----------------|
| $\bar{l}$ mm. (var. l) .   | 2.73 (1.264)   |
| $\bar{th}$ mm. (var. th) . | 1.36 (0.378)   |
| r .                        | 0.808          |
| a (var. a) .               | 0.547 (0.0104) |

TABLE 31. Statistics of the length ( $\bar{l}$ ) and maximum thickness ( $\bar{th}$ ) of 12 pedicle valves of *Skenidioides* cf. *costatus* Cooper.



TABLE 32

|                  |       |          |
|------------------|-------|----------|
| l mm. (var. l) . | 3.05  | (0.825)  |
| c mm. (var. c) . | 1.01  | (0.102)  |
| r .              | 0.932 |          |
| a (var. a) .     | 0.352 | (0.0014) |

TABLE 32. Statistics of the length of 14 brachial valves (l) and their cardinalia (c) of *Skenidioides* cf. *costatus* Cooper.

HORIZONS AND LOCALITIES. Gelli-grŷn Group : BB.24548 from calcareous ashes exposed in Ffridd Bach immediately south of Maes-meillion Farm ; all other specimens from calcareous ashes exposed on the east side of the central outlier of Rhiwlas Limestone on Creigiau Bychain.

DISCUSSION. *Skenidioides* is fairly common in the Gelli-grŷn Group and is quite distinctive, especially in its radial ornamentation. As can be seen from Tables 30-32, the subpyramidal pedicle valve was inherently wider than long and this was maintained throughout growth as was the relative depth of the valve. The radial ornamentation consists essentially of up to 17 costae with the median costa, forming the crest of the pedicle valve, having a mean wavelength of 0.5 mm. (range 0.45-0.65 mm.) compared with a mean wavelength of 0.3 mm. (range 0.2-0.35 mm.) for the lateral costae in 4 pedicle valves. But in pedicle valves between 2.0 and 3.0 mm. long the costellae 1a°, 2a°, 3ā, 3a° and 4a° split off from their parent primaries in 5/8, 7/8, 2/8, 5/8 and 2/7 valves respectively with 2a° invariably arising before 3a° and 4a° and even before 1a° in 5/7 valves. Internally, the most distinctive feature is the well developed cardinalia dominated by the strong brachiophore bases which converge onto the median septum of the brachial valve at almost one-third the length of the valve anterior of the dorsal umbo, a proportion that was maintained throughout growth.

These *Skenidioides* are at present inseparable from *S. costatus* Cooper (1956 : 493) from the Edinburg formation of Virginia. Certainly the relative proportions representing shell outline, profile and size of internal features of the American type specimens are all well within the ranges of those assessed for the Welsh stock, and in radial ornamentation, even to details of secondary branching, the two stocks are identical.

#### Family CREMNORTHIDAE nov.

DIAGNOSIS. Biconvex, costellate and dorsally sulcate orthaceids with short, curved interareas and unmodified delthyrium and notothyrium ; ventral muscle field subtriangular with wide adductor scar, dental lamellae, if present, short and receding ; cardinalia consisting of stout, trilobed cardinal process continuous with high, blade-like median septum, subtriangular in outline and extending to anterior margin, and pair of short, divergent brachiophores with bases curved laterally to define pair of semi-oval sockets.



Genus **CREMNORTHIS** nov.

DIAGNOSIS. Subcircular, biconvex shells with deep, subcarinate pedicle valve and strongly convex and sulcate brachial valve so that commissure is sharply sulcate antero-medianly and curved laterally with convex arcs facing dorsally ; radial ornamentation fascicostellate with angular costae and costellae ; ventral interarea curved, apsacline with open, narrow delthyrium ; dorsal interarea short, curved, anacline, notothyrium filled by cardinal process ; shell probably impunctate.

Ventral interior with obliquely disposed teeth ankylosed to floor of valve by thick deposits of secondary shell rather than discrete dental lamellae, pedicle callist well developed ; muscle field not extending much beyond umbonal cavity, subtriangular in outline with wide median adductor scar separating pair of diductor scars each of which consists of narrow, ventrally facing submedian lobe enclosed anteriorly by *vasculum medium* and lateral lobe impressed on the side of umbonal cavity ; pallial sinus pattern unknown except for a pair of divergent *vascula media*.

Dorsal interior with cardinalia dominated by massive cardinal process standing well above hinge-line and trilobed in arrangement with median crest separating ventral parts of areas for diductor insertion ; brachioophores, short, obliquely disposed and continuous with bases which curve laterally to define a pair of semi-elliptical sockets ; cardinal process continuous with blade-like median septum which extends to anterior margin and which must have been sufficiently high almost to make contact with pedicle valve along its antero-median half ; dorsal adductor field elongately oval, quadripartite impressed on either side of septum just anterior of cardinalia and further divided by narrowly divergent *vascula myaria*.

TYPE SPECIES. *Cremnorthis parva* sp. nov. from the Gelli-grîn Group.

DISCUSSION. The new genus is at present represented solely by the type species which itself is known only from a small number of internal and external moulds so that no original shell material has been recovered to determine whether the test was punctate or impunctate. Despite the coarseness of the Gelli-grîn calcareous ashes, however, the puncta of all dalmanellaceids recovered from the deposits were filled with ferric oxides and clays which adhered to the internal moulds as fine granules and the invariable absence of these suggests that the species was impunctate in the orthaceid manner : in any event it is sufficiently distinctive to be recognized without recourse to the condition of the shell. Among the orthaceids, closest comparison can be drawn with the contemporary *Phragmorthis* Cooper (1956 : 508-510) in the general aspect of the shell, in the nature of the ventral muscle field and especially in the presence of a high median septum. This similarity, however, may be an expression of convergence for the brachioophore bases do not converge on to the median septum as in *Phragmorthis* which also lacks the elaborate cardinal process and fascicostellate ornamentation of *Cremnorthis*. Indeed, in respect of most features, the new genus has more in common with certain Devonian dalmanellaceids like *Prokopia* (Havlíček 1956 : 118) although it differs, apart from its probable impunctate test, in both the style of ornamentation and the structure of the cardinal process, and the likeness is more probably the result of homeomorphy than affinity.



*Cremnorthis parva* gen. et sp. nov.

(Pl. 4, figs. 15-23 ; Text-fig. 9)

DIAGNOSIS. Subrectangular, strongly biconvex *Cremnorthis* with medianly sulcate brachial valve over two-thirds as long as wide and about three-tenths as deep as long and subcarinate pedicle valve nearly one-half as deep as long ; ventral interarea curved about one-tenth as long as pedicle valve and twice as long as dorsal interarea ; radial ornamentation fascicostellate with sharply angular costae and costellae about 4 per mm. at 2 mm. anterior of dorsal umbo, sectors I and II occurring within dorsal sulcus, external secondary costellae common in sectors II to V ; pedicle callist well developed, less than one-tenth as long as pedicle valve, ventral subtriangular muscle scar almost as long as wide and extending anteriorly for just over one-third the length of valve ; brachiophore bases widely splayed and strong, almost one-fifth as long as brachial valve and about two-fifths as long as wide ; dorsal median septum attaining a height of almost one-third the length of brachial valve in anterior half of its extent ; dorsal adductor scars impressed on either side of septum just anterior of brachiophore bases and extending anteriorly for almost three-quarters the length of valve.

|            |                                                               | length | width (mm.) |
|------------|---------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of brachial valve (BB.28923)                   | 2.3    | —           |
| PARATYPES. | Internal mould of brachial valve (BB.28896)                   | 3.0    | 4.0         |
|            | Internal mould of pedicle valve (BB.28897)                    | 3.6    | 4.2         |
|            | External mould of brachial valve (BB.28898)                   | 3.2    | 3.8         |
|            | External mould of pedicle valve (BB.28899)                    | 1.2    | 1.9         |
|            | External mould of conjoined valves, ventral aspect (BB.28900) | 3.5    | —           |

HORIZON AND LOCALITY. Gelli-grŷn Group : calcareous ashes exposed above limestone in the old quarry, 1,100 ft. west-south-west of Gelli-grŷn Farm.

DISCUSSION. The new species is at least generically distinguishable from contemporary brachiopods so that only some aspects of the diagnosis need further discussion. The mean percentage length relative to width, and depth relative to length of 6 dorsal external moulds (with variance) were respectively 68.8 (88.6) and 26.8 (20.6). The subcarinate pedicle valves were more strongly convex with a mean percentage depth relative to length (with variance) in 7 specimens of 48.1 (58.5). In the ventral internal moulds the conspicuous, narrow pedicle callist had a mean percentage length relative to the length of 4 specimens of 8.5 (range 8 to 9) while in 5 specimens the mean percentage length of the muscle field anterior to the umbo relative to the length of the valve and to its maximum width in ventral aspect were (with variances) 35.0 (39.0) and 95.6 (24.2) respectively. The robust



cardinalia formed prominent holes in the dorsal internal moulds and in 9 specimens the mean percentage length of the brachiphore bases relative to valve length (with variance) was 18.2 (11.13) while in 8 moulds the mean percentage length of the brachiphore bases relative to the maximum width of the sockets was 40.9 (variance 25.86).

The fascicostellate pattern is quite distinctive. In 3 brachial valves, 4 costellae occurred within 1 mm. at 2 mm. from the umbo and this order of wavelength is typical of the radial ornamentation except for a broad median costa occupying the crest of the pedicle valve. The pattern in the right halves of the brachial valves is typically 1, 2, 2a°, 3, 3a°, with 1ā, 2ā and 3ā occurring in 2/6, 3/6 and 2/4 specimens respectively, so that external secondary costellae are relatively well developed in the second and third sectors.

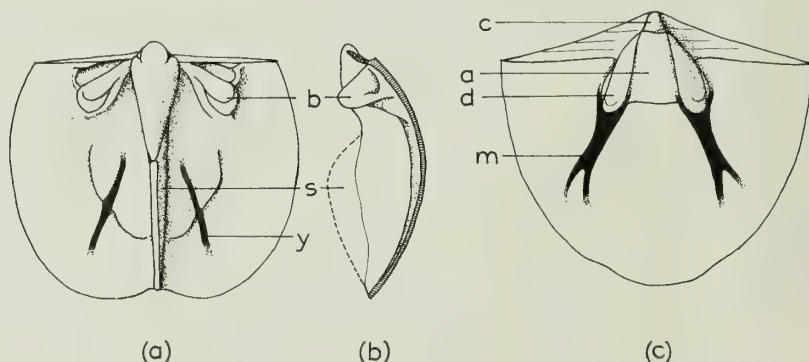


FIG. 9. The ventral (a) and lateral (b) aspects of a dorsal interior and the ventral internal mould (c) of *Cremnorchis parva* gen. et sp. nov.,  $\times 10$  approx.: a, adductor scar; b, brachiphore; c, pedicle callist; d, diductor scar; m, *vascula media*; s, septum; y, *vascula myaria*.

### Superfamily DALMANELLACEA Schuchert & Le Vene 1929

#### Family DALMANELLIDAE Schuchert & Le Vene 1929

#### Genus *DALMANELLA* Hall & Clarke 1892

TYPE SPECIES. *Orthis testudinaria* Dalman by original designation of Hall & Clarke (1892 : 205).

#### *Dalmanella modica* sp. nov.

(Pl. 4, figs. 24, 25; Pl. 5, figs. 1-7)

DIAGNOSIS. Subcircular, unequally biconvex *Dalmanella* with sulcate brachial valve about three-quarters as long as wide and almost one-fifth as deep as long and evenly convex pedicle valve just over one-third as deep as long; radial ornamentation costellate with modal count of 3 costellae per mm., 5 mm. anterior



of dorsal umbo, external secondary branching poorly developed in sectors I to IV ; dental lamellae divergent, extending anteriorly for just over one-fifth the length of pedicle valve, teeth strong ; adult ventral muscle field subcordate in outline slightly narrower than long with submedian diductor scars extending forward of umbo for less than one-third the length of pedicle valve and not enclosing broad median adductor scar ; adult cardinalia consisting of undifferentiated bilobed cardinal process and rod-like brachiophores supported by a pair of subparallel bases, extending forward for about one-fifth the length of brachial valve, and a pair of widely divergent socket plates, almost twice as wide as brachiophore bases are long ; median ridge short, fading anteriorly into broad internal crest of sulcus, and dividing adductor field into a pair of suboval scars about one-half as long as brachial valve ; pallial sinus patterns unknown.

|            |                                                             | length | width (mm.) |
|------------|-------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of conjoined valves (BB.28960)               | 12.0   | 14.0        |
| PARATYPES. | External and internal moulds of pedicle valve (BB.28961-62) | 7.0    | 7.0         |
|            | Internal mould of brachial valve (BB.29029)                 | 7.8    | 9.1         |
|            | Internal mould of brachial valve (BB.29131)                 | 8.5    | 9.5         |
|            | External and internal moulds of pedicle valve (BB.28963-64) | 10.0   | 11.0        |
|            | External mould of brachial valve (BB.24603)                 | 6.0    | 7.5         |
|            | External mould of brachial valve (BB.28966)                 | 9.5    | 11.5        |
|            | External mould of brachial valve (BB.28967)                 | 10.0   | 13.7        |

HORIZON AND LOCALITIES. Gelli-grŷn Group ; BB.28960, BB.24603 from calcareous ash crags beginning 75 ft. south of the east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28961-62 calcareous ashes exposed on the east side of the central outlier of Rhiwlas Limestone, Creigiau Bychain ; BB.29029, BB.29131, BB.28963-64 calcareous ashes cropping out on the north side of the track leading from Gelli-grŷn Farm, 1,000 ft. west-south-west of the farm, BB.28966-67 calcareous ash crags 700 ft. west-north-west of BM.1338.7, south side of Bryn Fig.

DISCUSSION. Isolated valves of *Dalmanella* are fairly common in the Gelli-grŷn Group and were referred by Bancroft (1945 : 193) to three distinct species—*D. horderleyensis* (Bancroft), *D. indica* (Whittington) and *D. leptæ* (Bancroft). The last species was founded on immature shells and is conspecific with *D. indica* so that one would anticipate *Dalmanella* from the Bala district as belonging to two distinct



morphological assemblages. All the moulds recovered however, are the remains of a homogeneous group which is unlike any known *Dalmanella* in a number of details and is accordingly described as a new species, *Dalmanella modica*.

In his account of the generic features of *Wattsella* (now accepted as synonymous with *Dalmanella*), Bancroft (1945 : 190) laid great emphasis on the co-existence of "normal" and "progressive" forms characterized by the predominance of externally and internally branching costellae respectively. Bancroft clearly believed that these two groups merited supra-specific recognition and although other studies (Williams & Wright, 1963 : 20) suggest such procedure to be unnecessary the segregation into normal and progressive stocks is a convenient guide to *Dalmanella* taxonomy. Thus, Table 33 shows the new species to differ significantly ( $p < .01$ ) from *D. horderleyensis* in the late origin of  $3a^\circ$  and  $4b^\circ$  in the manner comparable with *D. indica* (and *D. lepta*). But it also differs from these two ( $p < .01$ ) in the early development of  $2a^\circ$ , a characteristic it shares with *D. horderleyensis*. This comparison of course does not imply that the Gelli-grin shells were transitional between two species groups because patterns of branching are known to have been developed independently of one another in different sectors. On balance then, *D. modica* may be regarded as a progressive form as it also is in the rather fine texture of its costellate ornamentation because at a distance of 5 mm. anterior of the dorsal umbo, 2, 3 or 4 costellae per mm. were counted in 2, 17 and 14 brachial valves of *D. modica* compared with 0, 15 and 11 valves of *D. indica* and 9, 4 and 0 of *D. horderleyensis*.

TABLE 33

|                               |                                   | A         | B         | C        |
|-------------------------------|-----------------------------------|-----------|-----------|----------|
| 1 $\bar{a}$ $\bar{1}$ )       | 1 $\bar{b}$ .                     | 3/6 (1)   | 0/14 (1)  | 0/4 (1)  |
| 1 $\bar{b}$ )                 | 1 $\bar{a}$ .                     | 5/7 (1)   | 11/11     | 4/6      |
| 2 $\bar{b}$ $\bar{1}$ )       | 2 $\bar{a}$ .                     | 0/4       | 3/3       | 0/2      |
| 2 $\bar{c}$ )                 | 2 $a^\circ$ .                     | 1/6       | 5/5       | 0/2      |
| 3 $\bar{a}$ 1 $\bar{a}$ )     | 3 $a^\circ$ .                     | 9/14 (1)  | 19/23     | 3/25 (1) |
| 3 $\bar{c}$ )                 | 3 $a^\circ$ .                     | 10/15 (1) | 18/22     | 2/23 (2) |
| 3 $\bar{b}$ $\bar{1}$ )       | 3 $\bar{c}$ .                     | 3/10 (3)  | 3/8 (4)   | 3/3 (1)  |
| 3 $\bar{a}$ 1 $\bar{a}$ )     | 3 $\bar{a}$ $\bar{2}$ .           | 11/11 (3) | 7/8 (4)   | 2/5      |
| 4 $\bar{b}$ )                 | 4 $b^\circ$ .                     | 15/19 (1) | 11/15 (3) | 2/15     |
| 4 $\bar{a}$ $\bar{1}^\circ$ ) | 4 $\bar{a}$ $\bar{1}$ $\bar{a}$ . | 4/8       | 0/7       | —        |
| 4 $\bar{a}$ $\bar{1}^\circ$ ) | 4 $\bar{b}$ $\bar{1}$ .           | 6/6       | 0/5       | —        |
| 4 $\bar{a}$ 1 $\bar{a}$ )     | 4 $b^\circ$ .                     | 5/9 (1)   | 2/7       | —        |
| 3 $\bar{a}$ 1 $\bar{a}$ )     | 2 $\bar{a}$ $\bar{1}$ .           | 3/9 (2)   | 5/14      | —        |
| 3 $\bar{a}$ 1 $\bar{a}$ )     | 2 $a^\circ$ .                     | 10/12     | 12/12     | 0/1      |

TABLE 33. The proportions of the earlier insertion of 14 costellae relative to 14 others (with the number of valves in which both costellae originated at the same growth stage in brackets) for samples of *Dalmanella modica* sp. nov. (A), *Dalmanella indica* (Whittington) (B), and *Dalmanella horderleyensis* (Bancroft) (C).



TABLE 34

|                                     |   | A |                  |   |   | B                |  |
|-------------------------------------|---|---|------------------|---|---|------------------|--|
| $\bar{l}$ mm. (var. $l$ )           | . | . | 4.91 (8.773)     | . | . | 7.98 (8.024)     |  |
| $\bar{w}$ mm. (var. $w$ )           | . | . | 6.53 (14.275)    | . | . | 10.23 (10.417)   |  |
| $r$                                 | . | . | 0.985            | . | . | 0.933            |  |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | . | 1.436 (0.3105)   | . | . | 2.0176 (0.1185)  |  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) | . | . | 1.7319 (0.2889)  | . | . | 2.2776 (0.0953)  |  |
| $r_e$                               | . | . | 0.989            | . | . | 0.992            |  |
| $\alpha$ (var. $\alpha$ )           | . | . | 0.9646 (0.00064) | . | . | 0.8968 (0.00075) |  |

TABLE 34. Statistics of length ( $l$ ) and maximum width ( $w$ ) of 34 brachial valves of *Dalmanella modica* sp. nov. (A) and of 19 brachial valves of *Dalmanella indica* (Whittington) (B).

TABLE 35

|                                       |   |   | A               |   |   |                 | B |  |
|---------------------------------------|---|---|-----------------|---|---|-----------------|---|--|
| $\bar{l}$ mm. (var. $l$ )             | . | . | 7.09 (2.615)    | . | . | 8.53 (5.075)    |   |  |
| $\bar{th}$ mm. (var. $th$ )           | . | . | 1.33 (0.194)    | . | . | 1.55 (0.314)    |   |  |
| $r$                                   | . | . | 0.863           | . | . | 0.929           |   |  |
| $\log_e \bar{l}$ (var. $\log_e l$ )   | . | . | 1.9333 (0.0507) | . | . | 2.1097 (0.0677) |   |  |
| $\log_e \bar{th}$ (var. $\log_e th$ ) | . | . | 0.233 (0.1044)  | . | . | 0.3767 (0.1231) |   |  |
| $r_e$                                 | . | . | 0.867           | . | . | 0.917           |   |  |
| $\alpha$ (var. $\alpha$ )             | . | . | 1.435 (0.03007) | . | . | 1.348 (0.01807) |   |  |

TABLE 35. Statistics of length ( $l$ ) and thickness ( $th$ ) of 19 brachial valves of *Dalmanella modica* sp. nov. (A) and of 18 brachial valves of *Dalmanella indica* (Whittington) (B).

TABLE 36

|                                     |   |   | A                |   |   |                 | B |  |
|-------------------------------------|---|---|------------------|---|---|-----------------|---|--|
| $\bar{l}$ mm. (var. $l$ )           | . | . | 5.13 (10.44)     | . | . | 8.71 (3.218)    |   |  |
| $\bar{c}$ mm. (var. $c$ )           | . | . | 1.07 (0.369)     | . | . | 1.49 (0.127)    |   |  |
| $r$                                 | . | . | 0.938            | . | . | 0.845           |   |  |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | . | 1.4678 (0.3345)  | . | . | 2.1439 (0.0411) |   |  |
| $\log_e \bar{c}$ (var. $\log_e c$ ) | . | . | 0.0767 (0.2813)  | . | . | 0.371 (0.0555)  |   |  |
| $r_e$                               | . | . | 0.949            | . | . | 0.882           |   |  |
| $\alpha$ (var. $\alpha$ )           | . | . | 0.9171 (0.00209) | . | . | 1.162 (0.01364) |   |  |

TABLE 36. Statistics of length of brachial valves ( $l$ ) and length of cardinalia ( $c$ ) of 42 specimens of *Dalmanella modica* sp. nov. (A) and of 24 specimens of *Dalmanella indica* (Whittington) (B).



TABLE 37

|                                     |   | A               |   | B               |
|-------------------------------------|---|-----------------|---|-----------------|
| $\bar{l}$ mm. (var. l)              | . | 1.2 (0.271)     | . | 1.45 (0.134)    |
| $\bar{w}$ mm. (var. w)              | . | 2.17 (0.92)     | . | 2.81 (0.246)    |
| r                                   | . | 0.841           | . | 0.788           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | 0.096 (0.1725)  | . | 0.3405 (0.0621) |
| $\log_e \bar{w}$ (var. $\log_e w$ ) | . | 0.6855 (0.1784) | . | 1.0179 (0.0306) |
| $r_e$                               | . | 0.842           | . | 0.81            |
| $\alpha$ (var. $\alpha$ )           | . | 1.017 (0.01368) | . | 0.702 (0.00891) |

TABLE 37. Statistics of length (l) and maximum width (w) of the cardinalia of 24 brachial valves of *Dalmanella modica* sp. nov. (A) and of 21 brachial valves of *Dalmanella indica* (Whittington) (B).

TABLE 38

|                          |   | A                |   | B                |
|--------------------------|---|------------------|---|------------------|
| $\bar{l}$ mm. (var. l)   | . | 7.74 (4.506)     | . | 8.72 (3.237)     |
| $\bar{sc}$ mm. (var. sc) | . | 3.84 (0.902)     | . | 4.53 (1.071)     |
| r                        | . | 0.918            | . | 0.921            |
| a (var. a)               | . | 0.4474 (0.00165) | . | 0.5753 (0.00279) |

TABLE 38. Statistics of length of brachial valve (l) and extension of adductor scars anterior of the umbo (sc) of 21 specimens of *Dalmanella modica* sp. nov. (A) and of 20 specimens of *Dalmanella indica* (Whittington) (B).

TABLE 39

|                          |   | A                |   | B                |
|--------------------------|---|------------------|---|------------------|
| $\bar{l}$ mm. (var. l)   | . | 7.1 (8.962)      | . | 6.49 (7.689)     |
| $\bar{th}$ mm. (var. th) | . | 2.45 (0.846)     | . | 1.93 (0.864)     |
| r                        | . | 0.929            | . | 0.922            |
| a (var. a)               | . | 0.3072 (0.00129) | . | 0.3351 (0.00168) |

TABLE 39. Statistics of length (l) and thickness (th) of 12 pedicle valves of *Dalmanella modica* sp. nov. (A) and of 12 pedicle valves of *Dalmanella indica* (Whittington) (B).

TABLE 40

|                                       |   | A               |   | B               |
|---------------------------------------|---|-----------------|---|-----------------|
| $\bar{l}$ mm. (var. l)                | . | 5.76 (6.941)    | . | 6.92 (6.336)    |
| $\bar{sc}$ mm. (var. sc)              | . | 1.82 (0.853)    | . | 2.34 (1.171)    |
| r                                     | . | 0.959           | . | 0.969           |
| $\log_e \bar{l}$ (var. $\log_e l$ )   | . | 1.5693 (0.3632) | . | 1.8724 (0.1239) |
| $\log_e \bar{sc}$ (var. $\log_e sc$ ) | . | 0.484 (0.2295)  | . | 0.7495 (0.2013) |
| $r_e$                                 | . | 0.969           | . | 0.962           |
| $\alpha$ (var. $\alpha$ )             | . | 0.795 (0.00257) | . | 1.275 (0.00638) |

TABLE 40. Statistics of length of pedicle valve (l) and length of ventral muscle field (sc) of 17 specimens of *Dalmanella modica* sp. nov. (A) and of 21 specimens of *Dalmanella indica* (Whittington) (B).



TABLE 41

|                                     | A |   |        |           | B |                  |
|-------------------------------------|---|---|--------|-----------|---|------------------|
| $\bar{l}$ mm. (var. $l$ )           | . | . | 1.83   | (0.826)   | . | 2.34 (1.211)     |
| $\bar{w}$ mm. (var. $w$ )           | . | . | 1.77   | (0.603)   | . | 2.27 (0.634)     |
| $r$                                 | . | . | 0.911  | .         | . | 0.966            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | . | 0.4939 | (0.2207)  | . | 0.7503 (0.1997)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) | . | . | 0.4827 | (0.1766)  | . | 0.7618 (0.1159)  |
| $r_e$                               | . | . | 0.924  | .         | . | 0.975            |
| $\alpha$ (var. $\alpha$ )           | . | . | 0.8971 | (0.00905) | . | 0.7619 (0.00159) |

TABLE 41. Statistics of length ( $l$ ) and maximum width ( $w$ ) of the ventral muscle field of 15 specimens of *Dalmanella modica* sp. nov. (A) and of 20 specimens of *Dalmanella indica* (Whittington) (B).

TABLE 42

|                             | A |   |        |           | B |                  |
|-----------------------------|---|---|--------|-----------|---|------------------|
| $\bar{l}$ mm. (var. $l$ )   | . | . | 6.65   | (7.393)   | . | 6.92 (6.336)     |
| $\bar{dl}$ mm. (var. $dl$ ) | . | . | 1.39   | (0.254)   | . | 1.51 (0.36)      |
| $r$                         | . | . | 0.947  | .         | . | 0.935            |
| $a$ (var. $a$ )             | . | . | 0.1854 | (0.00175) | . | 0.2383 (0.00038) |

TABLE 42. Statistics of length of pedicle valve ( $l$ ) and anterior extension of dental lamellae ( $dl$ ) of 22 specimens of *Dalmanella modica* sp. nov. (A) and of 21 specimens of *Dalmanella indica* (Whittington) (B).

In other morphological features too, the new species is superficially like *D. indica*, a sample of which was obtained from the type locality (Bancroft 1945 : 195) for comparative purposes. The results of nine analyses of relative growth of both species are given in Tables 34-42. In the outline and profile of the brachial valves, the relative length of the cardinalia, the profile of the pedicle valve and the outline of the ventral muscle scar, the two samples show no noteworthy differences in either growth ratios or inherent proportions. The increase in width of the cardinalia (that is the lateral expansion of the fulcral plates) was, however, significantly faster in *D. modica* than in *D. indica* ( $0.02 > p > 0.01$ ) while the anterior migration of the dorsal adductor scars of *D. modica* was significantly slower ( $0.05 > p > 0.02$ ). Discernible differences also occurred in the pedicle valves. Thus, although the outlines of the ventral muscle scars were similar, that of *D. modica* did not extend anteriorly as fast as that of *D. indica* ( $p < 0.001$ ) and so was absolutely shorter relative to the valve throughout growth as were also the dental lamellae of *D. modica* ( $0.05 > p > 0.02$ ). Despite many similarities then the Gelli-grin shells are quite distinct from *D. indica* especially in the early occurrence of external branching in the second sector of the brachial valve, in the fast lateral growth of the fulcral plates relative to the forward growth of the supporting plates and in the slower



anterior expansion of the ventral muscle field, the dental lamellae and the dorsal adductor scars relative to the growth of the shell.

Genus **HOWELLITES** Bancroft 1954

DIAGNOSIS (emended). Subcircular, unequally biconvex to plano-convex shells with sulcate brachial valve ; radial ornamentation finely costellate with first to third order costellae branching internally more commonly than externally. Ventral interarea long, curved and apsacline with open delthyrium ; dorsal interarea short curved, anacline, notothyrium filled by cardinal process ; shell punctate.

Ventral interior with large teeth supported by well developed dental lamellae ; muscle field subtriangular to bilobed in outline with submedian diductor lobes not enclosing median adductor scar ; ventral pallial sinus pattern lemniscate, *vascula media* slightly divergent and greatly divided.

Dorsal interarea with stout undifferentiated bilobed cardinal process ; brachio-phores short, rod-like with their bases slightly to greatly divergent relative to their tops, fulcral plates sporadically developed ; dorsal adductor scar quadripartite, elongately oval ; pallial sinus pattern lemniscate.

TYPE SPECIES. *Resserella* (*Howellites*) *striata* Bancroft.

DISCUSSION. The taxonomic status of *Howellites*, which has been fully reviewed by Williams & Wright, 1963, may be summarized briefly as follows. The name was proposed by Bancroft (1945 : 203) for a group of dalmanellids which differed from *Resserella* (*Resserella*) Bancroft 1928, as conceived by him, mainly in "the presence of distinct fulcral plates and supporting plates" in immature brachial valves. It can be shown, however, that the differentiation of fulcral plates was not as fundamental to the growth of the cardinalia as Bancroft maintained (Williams & Wright 1963 : 9) and in any event occurred, although less commonly, in species of *Resserella* s.s. ; and since other differences given by Bancroft, like the stronger convexity of the brachial valves of *Howellites* spp., are not relevant to supra-specific classification, there was no justification for subgeneric segregation. Although Bancroft had proposed *Resserella*, he designated an assortment of shells, described by J. de C. Sowerby as *Orthis canalis*, as type species and when Schuchert & Cooper (1932 : 126) chose the lectotype they cited a specimen from the Wenlock Shale which later proved to be very close to *Orthis elegantula* Dalman, the type species of their genus *Parmorthis*. *Resserella* is therefore a synonym of *Parmorthis* but, since there is no generic difference between those Caradocian dalmanellids formerly known as "*Orthis canalis*" and given the varietal name *antiquior* by M'Coy (1852) and species of *Howellites*, *Howellites* can now be used in place of *Resserella*.

*Howellites* is certainly close to *Paucicrura* Cooper 1956, in many features but the invariable development of a differentially trilobed cardinal process in species assigned to the latter genus compared with the undifferentiated bilobed process of British stocks serves to distinguish between the two.



***Howellites striata* Bancroft**

(Pl. 5, figs. 8-18)

1945 *Resserella* (*Howellites*) *striata* Bancroft : 204, pl. 26, figs. 2-10, pl. 27, figs. 13-15, pl. 28, figs. 1-3.1945 *Resserella* (*Howellites*) *striata lineata* Bancroft : 205, pl. 26, figs. 11, 12, pl. 28, fig. 4.1945 *Resserella* (*Howellites*) *intermedia expectata* Bancroft : 206, pl. 27, figs. 5-9, pl. 28, figs. 7, 8.

DIAGNOSIS (emended). Subcircular, unequally biconvex *Howellites* with evenly convex sulcate brachial valve less than three-quarters as long as wide and less than one-seventh as deep as long and pedicle valve just over one-third as deep as long ; radial ornamentation finely costellate with modal count of 4 costellae per mm., 5 mm. anterior of dorsal umbo, external branching rarely occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, less than one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for about two-fifths the length of valve and about four-fifths as wide as long in adult stages of growth ; cardinalia well defined with divergent brachiphore bases extending anteriorly for about one-fifth the length of brachial valve, and less than two-thirds as long as wide, dorsal adductor scars extending forward for about three-fifths the length of valve.

## MATERIAL (Figured).

|                                                     | length | width (mm.) |
|-----------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve (BB.28925)          | 10.0   | 10.0        |
| Internal mould of brachial valve (BB.28926)         | 8.0    | 10.2        |
| External mould of brachial valve (BB.28927)         | 9.0    | 12.0        |
| Internal mould of brachial valve (BB.28928)         | 8.0    | 10.2        |
| Deformed internal mould of pedicle valve (BB.28929) | 8.8    | 8.0         |
| External mould of brachial valve (BB.28930)         | 5.5    | —           |
| External mould of pedicle valve (BB.28931)          | 11.0   | —           |
| Internal mould of brachial valve (BB.24650)         | 10.5   | 12.0        |
| Internal mould of pedicle valve (BB.24652)          | 9.5    | 10.0        |
| External mould of brachial valve (BB.24650)         | 8.3    | 10.0        |
| External mould of pedicle valve (BB.24651)          | 8.0    | —           |

HORIZON AND LOCALITIES. Allt Ddu Group : BB.28925-27 from siltstone crags in the scarp by the south side of the wall about 880 ft. east of Ty'n-y-cefn Farm, Craig y Gath (type locality of *H. striata* Bancroft 1945 : 205) ; BB.28928-31 from siltstone crags at the wall junction about 1,000 ft. east of Ty'n-y-cefn Farm, Craig



y Gath (type locality of *H. striata lineata* Bancroft 1945 : 205) ; BB.24650-52, from exposures in the gutter section on Craig y Gath, 3,400 ft. south of Glyn Mawr (type locality of *H. intermedia expectata* Bancroft 1945 : 206).

***Howellites intermedia* Bancroft**

(Pl. 6, figs. 1-5)

1945 *Resserella* (*Howellites*) *intermedia* Bancroft : 205, pl. 27, figs. 1-4, pl. 28, figs. 5, 6.

DIAGNOSIS (emended). Subcircular, unequally biconvex *Howellites* with evenly convex, sulcate brachial valve about three-quarters as long as wide and about one-eighth as deep as long and pedicle valve over one-third as deep as long ; radial ornamentation finely costellate with modal count of 4 costellae per mm., 5 mm. anterior of dorsal umbo, external branching rarely occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, less than one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for just over two-fifths the length of valve and over four-fifths as wide as long in adult stages of growth ; cardinalia well defined with divergent brachioophore bases extending anteriorly for about one-fifth the length of brachial valve and just over three-fifths as long as wide, dorsal adductor scars extending forward of umbo for over one-half the length of valve.

MATERIAL (Figured).

|                                                        | length | width (mm.) |
|--------------------------------------------------------|--------|-------------|
| Internal mould of brachial valve<br>(BB.28936)         | 7.0    | 10.2        |
| Deformed internal mould of<br>pedicle valve (BB.28937) | 10.0   | 9.5         |
| External mould of brachial valve<br>(BB.28938)         | —      | 9.5         |
| External mould of brachial valve<br>(BB.28939)         | 8.3    | —           |
| External mould of pedicle valve<br>(BB.28940)          | 9.0    | 11.0        |

HORIZON AND LOCALITY. Allt Ddu Group : all specimens from siltstone crags on Craig y Gath about 120 yds. east of the ford 2,200 ft. south of Ty'n-y-Cefn (type locality 4a, 2, of *H. intermedia* Bancroft 1945 : 205).

***Howellites ultima* Bancroft**

(Pl. 6, figs. 6-12)

1945 *Resserella* (*Howellites*) *ultima* Bancroft : 209, pl. 27, figs. 10-12, pl. 28, figs. 9, 10.

DIAGNOSIS (emended). Subcircular, unequally biconvex *Howellites* with evenly convex, sulcate, brachial valve about three-quarters as long as wide and about one-sixth as deep as long and pedicle valve over one-third as deep as long ; radial ornamentation rather finely costellate with modal count of 4 costellae per mm., 5 mm. anterior of dorsal umbo, external branching commonly occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, about one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for about two fifths the length of valve and over three-quarters as wide as long in



adult stages of growth ; cardinalia well-defined with divergent brachiophore bases extending anteriorly for over one-fifth the length of brachial valve and less than two-thirds as long as wide ; dorsal adductor scars extending forward of umbo for less than three-fifths the length of valve.

| MATERIAL (Figured).                         | length | width (mm.) |
|---------------------------------------------|--------|-------------|
| Internal mould of pedicle valve (BB.28941)  | 9.0    | 10.1        |
| Internal mould of brachial valve (BB.28942) | 3.5    | 4.3         |
| Internal mould of brachial valve (BB.28943) | 9.0    | —           |
| Internal mould of brachial valve (BB.28944) | 9.5    | 11.8        |
| External mould of brachial valve (BB.28945) | 4.2    | 5.5         |
| External mould of brachial valve (BB.28946) | 8.2    | 10.5        |
| External mould of pedicle valve (BB.28947)  | 8.5    | 10.5        |

HORIZON AND LOCALITY. All specimens from siltstone exposures about 80 ft. north of the gutter on Craig y Gath (type locality of *H. ultima* Bancroft 1945 : 209).

### *Howellites antiquior* (M'Coy)

(Pl. 6, figs. 13–19, Pl. 7, figs. 1, 2, 5, 6)

1839 *Orthis canalis* J. de C. Sowerby in Murchison : 640, pl. 20, fig. 8, *non* p. 630, pl. 13, fig. 12a.

1852 *Orthis canalis* Sowerby var.  $\alpha$  *antiquior* M'Coy : 217.

1928a *Resserella canalis* (Sowerby) Bancroft : 54 pars.

1959 *Paucicrura sowerbii* Cave & Dean : 295, pl. 53, figs. 7–11.

DIAGNOSIS (emended). Subcircular, unequally biconvex to almost plano-convex *Howellites*, brachial valve with variably defined sulcus dependent on evenness of convexity, about three-quarters as long as wide and less than one-seventh as deep as long, pedicle valve over two-fifths as deep as long ; radial ornamentation finely costellate with counts of 4 or 5 costellae per mm., 5 mm. anterior of dorsal umbo, external branching rarely occurring earlier than internal in sectors I to IV ; dental lamellae well developed, slightly divergent, less than one-quarter as long as pedicle valve, ventral muscle scar extending anteriorly for less than two-fifths the length of valve and less than four-fifths as wide as long in adult stages of growth ; cardinalia well-defined with divergent brachiophore bases extending anteriorly for about one-fifth the length of brachial valve and over one-half as long as wide, dorsal adductor scars extending forward for over one-half the length of valve.

| MATERIAL (Figured).                                            | length | width (mm.) |
|----------------------------------------------------------------|--------|-------------|
| Internal mould of conjoined valves (ventral aspect) (BB.28948) | 9.0    | 9.5         |
| Deformed internal mould of pedicle valve (BB.28949)            | 9.5    | 8.5         |



| MATERIAL (Figured) ( <i>continued</i> )        | length | width (mm.) |
|------------------------------------------------|--------|-------------|
| Internal mould of brachial valve<br>(BB.28950) | 8.5    | 11.0        |
| Internal mould of brachial valve<br>(BB.28951) | 6.3    | 7.5         |
| External mould of brachial valve<br>(BB.28952) | 8.2    | 11.5        |
| External mould of brachial valve<br>(BB.28953) | 9.5    | —           |
| External mould of pedicle valve<br>(BB.25043)  | 10.5   | 12.0        |
| Internal mould of brachial valve<br>(BB.28955) | 10.0   | —           |
| Internal mould of pedicle valve<br>(BB.28956)  | 10.0   | 12.3        |
| External mould of pedicle valve<br>(BB.28957)  | 10.0   | —           |
| External mould of brachial valve<br>(BB.28958) | 8.0    | 10.5        |

HORIZON AND LOCALITIES. Gelli-grŷn Group : BB.28948-49, BB.28951, BB.28953 from calcareous ashes exposed above the limestone in old quarries in Ffridd Bach, south of Maes-meillion ; BB.25043 from calcareous ash crags beginning 75 ft. south of east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28950, BB.28952 from calcareous ash crags 700 ft. west-north-west of BM.1338.7, south side of Bryn Pig.

The four specimens (BB.28955-58) which were collected from Lower Longvillian siltstones exposed on Gallt-yr-ancr, 440 yds. north of west from Dyffryn, one-half mile south-west of Meifod Church, the type locality for the species, have been figured for comparison with *Howellites antiquior* from the Gelli-grŷn Group. Data derived from a sample composed of *Howellites* from the Lower Longvillian rocks of Gallt-yr-ancr and also of the quarry, 200 yds. east-north-east of Bwlch-y-Cibau Church (locality 38 of Whittington 1938a : 448), are given in Tables 43-53. The sample is indistinguishable from that consisting of the Gelli-grŷn *Howellites* and the two assemblages are considered to be conspecific.

DISCUSSION. The dalmanellids found in the Allt Ddu and Gelli-grŷn rocks consist mainly of sorted assemblages of *Howellites*. Bancroft (1928 : 487) listed those recovered from the Gelli-grŷn Group as "*Dalmanella (canalis) Group*" and, as is shown in Tables 43-53, there is no significant difference in any of 11 characters between these and a sample of *Howellites antiquior* (M'Coy) from the Lower Longvillian of the Meifod District so that henceforth the Gelli-grŷn shells will be referred to as *Howellites antiquior*. The Allt Ddu dalmanellids collected by Bancroft were subsequently (1945 : 204-209) allocated by him to five species and subspecies which, arranged in stratigraphical sequence, are *H. striata*, *H. striata lineata*, *H. intermedia*, *H. intermedia expectata* and *H. ultima*. Bancroft recognized



that he was contriving to classify a series of closely related stocks but he drew distinctions between them on such characters as absolute size, a meaningless difference in water sorted assemblages, the fineness of radial ornamentation and above all the earlier or later origin of internally branching costellae relative to certain external ones belonging to the same sectors. His analyses were presented in table form (Bancroft 1945 : 204) and purported to show a progressive trend in the earlier insertion of external costellae from sector I to sector IV of the brachial valves occurring at successively higher horizons. This classification suffered from two defects (Williams & Wright 1963 : 22). First, Bancroft did not subject his data to any tests of significance so that such patterns of ornamentation may not have been sufficiently different to merit the systematic recognition proffered by him. Secondly, the presentation of his data in percentage form and without hint of the actual numbers of brachial valves involved, may have inadvertently concealed the use of samples too small to be reliable and an examination of his collections, now preserved in the British Museum, in fact confirmed that they were mostly inadequate for the finely drawn discriminations he proposed. Accordingly, with the exception of *Howellites intermedia expectata*, the locality for which could not be found, larger collections of topotypic material were obtained for all the species and subspecies described by Bancroft and the data given in Tables 43-53 are based on the newer collections as well as those of Bancroft.

Table 52 shows the distribution of costellae per mm. at a standard distance of 5 mm. anterior of the umbo, for the various species assigned to *Howellites*. In every sample the modal count was 4 per mm. and although there is some variation from 3 to 6 costellae per mm. it is misleading to claim, for example, that *H. intermedia expectata* is more coarsely ribbed than *H. intermedia* (Bancroft 1945 : 208) and indeed on this character alone there is no difference between any of the six species and subspecies listed.

In an attempt to cover any possible changes in the arrangement of the radial ornamentation, 27 ribbing associations were examined for all samples. Five of these associations, essentially reflecting the proportions of internal and external branching in the first four sectors, proved to be sufficiently variable to warrant comparison by exact probability methods, and Table 53 gives the actual proportions determined for all species and subspecies as well as those of *H. cf. ultima* from Bancroft's locality 4b9 and of *H. cf. striata* from mudstones of the Lower Allt Ddu Group exposed in a field about 300 yds. north-north-east of Ty'n-y-bryn Farm where the species is associated with *Dinorthis berwynensis* (Whittington). Chi-squared tests show that neither the relatively high incidence of  $\bar{1} \bar{1} \bar{1} \bar{1} \bar{1} \bar{1} \bar{1} \bar{1} \bar{1} \bar{1}$  nor the relatively low one of  $\bar{2} \bar{2} \bar{2} \bar{2} \bar{2} \bar{2} \bar{2} \bar{2} \bar{2} \bar{2}$  for *H. ultima* is important but that the low proportions of  $\bar{3} \bar{3} \bar{3} \bar{3} \bar{3} \bar{3} \bar{3} \bar{3} \bar{3} \bar{3}$  and  $\bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4}$  and the high ones for  $\bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4} \bar{4}$  are highly significant ( $p < .001$ ) for both *H. ultima* and *H. cf. ultima*. On the basis of radial ornamentation then there are only two distinct stocks—*H. ultima* (together with *H. cf. ultima*) and a pool of the remaining species which cannot be distinguished from one another on this character alone. Further, there are no trends leading to the predominance of external branching in any sector ; *H. ultima* is sharply dissociated from both



the younger *H. antiquior* and the older *H. intermedia expectata* and is not the climax of any gradual change.

There may, of course, have been other morphological differences resulting from changes in differential growth which had not been detected by Bancroft but which were none the less systematically important. Nine bivariate analyses, leading to estimates of growth ratios "a" or " $\alpha$ " and, if necessary, also inherent shape, "b" or " $\beta$ ", have therefore been conducted for each of the seven samples. These covered most if not all of the morphological variations which are normally employed in taxonomy and they are set out in Tables 43-51. In all, 135 comparisons were required to discover what difference existed. Twenty-three of these could not be completed because the coefficient of correlation,  $r$ , was not significant due to the small size of one or both samples; ten showed that significant differences ( $p < .05$ ) existed in either the growth ratios or inherent shapes: while no differences were found in any of the remaining 102 comparisons. The most striking conclusion then, is that the samples, drawn as they were from about 1,200 ft. of mudstones and ashes, were extremely conservative in most aspects of relative growth.

Thus in the growth of the cardinalia (Tables 48, 50), analysis showed that the process was mainly a simple one with the brachioophores expanding anteriorly by about one-fifth the forward growth of the brachial valve and laterally at almost twice the rate of anterior increment. Similarly the ventral muscle field tended to expand anteriorly by less than one-half the increase in valve length (Table 49), but allometry affected some samples so that the anterior encroachment of the muscle field became accelerated in adult stages of growth. This acceleration was more obvious in the changes in the outline of the ventral scar (Table 47) because in young valves the scars tended to be slightly wider than long whereas during subsequent growth, the accelerating anterior expansion gave the average lateral encroachment as only about four-fifths the forward one. In all four attributes the variability inherent to the samples, small though it is—the coefficient of correlation is at least 0.8 for all compared samples—is sufficient to account for any shifts in the growth axis or for differences in residual shape so that no important change took place in the growth and disposition of either cardinalia or the ventral muscle field.

In the remaining five aspects of relative growth significant differences did occur. Taking the maximum length and width as indices of outline (Table 43) it can be shown that the brachial valves, although affected by allometry in some samples, tended to expand laterally about one-fifth as fast again as their anterior expansion. *H. intermedia*, however, differed from all other samples except that of *H. striata*, in a significantly faster growth in width relative to length. Now *H. striata* is much more variable than other samples of comparable size. It is indistinguishable in every respect from *H. striata lineata* which may be collected from a crag about 25 ft. above the one yielding *H. striata* and if, on the reasonable assumption that both samples represent a homogeneous morphological assemblage, these two samples are pooled, the revised growth ratio differs significantly from that of *Howellites intermedia*. The depth of the brachial valve relative to length, is difficult to measure because many of the valves collapsed during burial, which accounts for the small



size of the samples. There was also a great deal of variation during growth in that young shells tended to be much more convex than adult ones and this allometric effect is characteristic of most samples. They are all, however, comparable with an average increase in depth of about one-eighth the anterior expansion of the valve, except for *H. intermedia* which became deeper at about the same rate as *H. ultima* but was significantly more convex in its residual profile. Dorsal adductor scars are commonly deeply impressed on the valve floor even in young shells and although the anterior expansion of the muscle field relative to valve length tended to accelerate during adult stages of growth in all samples compared with *H. antiquior*, only in *H. intermedia* and *H. striata lineata* was the difference significant. The relative expansion of the adductor scar of *H. striata* was again more variable than in other

|                                |                               |                           |                                |                      |                           |
|--------------------------------|-------------------------------|---------------------------|--------------------------------|----------------------|---------------------------|
| <i>H. ultima</i>               | f                             |                           |                                |                      |                           |
| <i>H. intermedia expectata</i> |                               | f                         |                                |                      |                           |
| <i>H. intermedia</i>           | a                             | a<br>ef<br>c <sub>1</sub> | b <sub>2</sub> a <sub>1</sub>  |                      |                           |
| <i>H. striata lineata</i>      |                               | f                         |                                | a <sub>1</sub>       |                           |
|                                | b <sub>1</sub> c <sub>1</sub> |                           |                                | a <sub>1</sub>       |                           |
| <i>H. striata</i>              |                               | f                         |                                |                      |                           |
|                                | d <sub>1</sub>                |                           |                                |                      |                           |
|                                | <i>H. antiquior</i>           | <i>H. ultima</i>          | <i>H. intermedia expectata</i> | <i>H. intermedia</i> | <i>H. striata lineata</i> |

FIG. 10. The distribution of significant differences between any two named species of *Howellites* where a and b respectively represent the relative width and depth of the brachial valve, c the relative length of the dorsal adductor scars, d the relative depth of the pedicle valve, e the relative length of the dental lamellae and f the early insertion of external costellae: lower case figures 1 or 2 respectively indicate significant differences in growth rate or inherent shape.



samples but in this attribute neither the growth ratio nor the residual shape of a pooled assemblage of *H. striata* and *H. striata lineata* differed significantly from those of *H. antiquior*.

Two characters of the pedicle valve remain to be discussed. The anterior growth of the divergent dental lamellae of all samples proceeded at about one-quarter the rate of the anterior expansion of the pedicle valve, except for the dental lamellae of *H. ultima*, which grew at a sufficiently faster rate to be significantly different from the slowest expansion found among the samples, namely that of *H. intermedia*. The last feature involving changes in the profile of the pedicle valve, is probably the most interesting because it is the only one to show a progressive shift in the growth ratios from the oldest sample (that of *H. striata*) to the youngest (*H. antiquior*). The growth was mostly simple without allometric complications and involving an increase from a deepening of the valve at just over one-quarter to just under one-half the anterior expansion. The sub-carinate pedicle valves of *H. antiquior*, therefore, differ significantly from the more uniformly convex valves of *H. striata* and *H. striata lineata*, in that they deepened faster relative to length.

The implications of all these comparisons can best be summarized in diagrammatic form (Text-fig. 10). Bearing in mind that eleven characters of shell morphology have been involved in testing the homogeneity of the seven samples, the differences are really minor, yet persistent enough to suggest that some of Bancroft's species ought to be retained. *H. ultima* differs from all other assemblages in the early development of externally branching costellae in sectors III and IV; it further differs from *H. intermedia* in the outline and profile of the brachial valve and in the relatively longer dental lamellae of the pedicle valve. *H. intermedia* may likewise be dissociated from other samples, assuming that *H. striata* and *H. lineata* belong to the same stock, in being relatively wider. It also differs from *H. antiquior* in the faster expansion of the dorsal adductor scars. In fact *H. ultima* and *H. intermedia* are so sharply distinct from other *Howellites* that one is tempted to think of them as fossil vestiges of two distinct species contemporaneous with the *H. striata-antiquior* complex and introduced briefly into the basin of deposition by changes in current direction. This assumption would explain the very close similarity between the four remaining samples. *H. antiquior* differs from both *H. striata* and *H. striata lineata* only in the greater relative depth of the pedicle valves and from the latter also in the relatively slower anterior spread of the dorsal adductor field. The *H. intermedia expectata* sample is unfortunately one affording no reliable data for the most vital attribute in this systematic procedure, namely the relative depth of the pedicle valve. In other crucial features it is clearly unrelated to *H. intermedia* but is indistinguishable from either *H. striata* s.l. or *H. antiquior*: provisionally the sample is classified with the former species.

In retrospect it is evident that Bancroft's taxonomic treatment of *Howellites* was unnecessarily discriminating. On radial ornamentation alone only *H. ultima* is distinguishable from *H. antiquior* and recourse to other, more subtle morphological changes becomes essential to preserve *H. intermedia* and *H. striata* (embracing *H. striata lineata* and *H. intermedia expectata*).



TABLE 43

|                          | n | A         | B         | C         | D         | E         | F         | G         |
|--------------------------|---|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
|                          | . | 29        | 94        | 62        | 15        | 50        | 46        | 21        |
| $\bar{l}$ mm.            | . | 6.97      | 4.98      | 5.29      | 6.59      | 5.01      | 5.04      | 4.83      |
| (var. l)                 | . | (5.2)     | (5.409)   | (6.079)   | (4.264)   | (5.675)   | (5.667)   | (2.942)   |
| $\bar{w}$ mm.            | . | 8.67      | 6.59      | 7.03      | 8.33      | 6.72      | 6.72      | 6.69      |
| (var. w)                 | . | (6.44)    | (7.714)   | (8.722)   | (5.536)   | (9.96)    | (8.553)   | (5.77)    |
| r.                       | . | 0.973     | 0.988     | 0.99      | 0.985     | 0.987     | 0.993     | 0.901     |
| a                        | . | —         | 1.194     | —         | 1.14      | 1.325     | —         | 1.4       |
| (var. a)                 | . | —         | (0.00037) | —         | (0.00297) | (0.00087) | —         | (0.01942) |
| $\log_e \bar{l}$         | . | 1.8904    | 1.5069    | 1.5677    | 1.8387    | 1.5091    | 1.5167    | 1.5155    |
| (var. $\log_e \bar{l}$ ) | . | (0.1014)  | (0.197)   | (0.1962)  | (0.0938)  | (0.2045)  | (0.2013)  | (0.1185)  |
| $\log_e \bar{w}$         | . | 2.1183    | 1.8032    | 1.8691    | 2.0814    | 1.8052    | 1.8184    | 1.8416    |
| (var. $\log_e \bar{l}$ ) | . | (0.0827)  | (0.1648)  | (0.1622)  | (0.077)   | (0.1997)  | (0.1733)  | (0.1211)  |
| $r_e$                    | . | 0.973     | 0.99      | 0.995     | 0.973     | 0.996     | 0.998     | 0.922     |
| $\alpha$                 | . | 0.9031    | 0.9146    | 0.9092    | 0.906     | 0.9882    | 0.9279    | 1.011     |
| (var. $\alpha$ )         | . | (0.00161) | (0.00018) | (0.00014) | (0.00337) | (0.00016) | (0.00008) | (0.00807) |

TABLE 43. Statistics of the length (l) and maximum width (w) of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 44

|                            | A        | B         | C        | D       | E         | F         | G        |
|----------------------------|----------|-----------|----------|---------|-----------|-----------|----------|
| n                          | I6       | 23        | 24       | 4       | I6        | IO        | 9        |
| l mm.                      | 7.13     | 6.15      | 6.18     | 7.63    | 5.93      | 6.72      | 5.87     |
| (var. l)                   | (2.241)  | (4.825)   | (4.943)  | (3.623) | (3.753)   | (3.016)   | (3.39)   |
| th mm.                     | 0.76     | 0.94      | 1.03     | 1.3     | 0.72      | 0.96      | 0.9      |
| (var. th)                  | (0.061)  | (0.214)   | (0.159)  | (0.097) | (0.055)   | (0.076)   | (0.0675) |
| r.                         | 0.758    | 0.841     | 0.82     | 0.53    | 0.825     | 0.665     | 0.545    |
| a                          | —        | —         | —        | —       | 0.121     | 0.1587    | —        |
| (var. a)                   | —        | —         | —        | —       | (0.00035) | (0.00176) | —        |
| log <sub>e</sub> l         | 1.9428   | 1.7563    | 1.7602   | —       | 1.7293    | 1.8726    | —        |
| (var. log <sub>e</sub> l)  | (0.043)  | (0.1203)  | (0.1222) | —       | (0.1014)  | (0.065)   | —        |
| log <sub>e</sub> th        | -0.3243  | -0.1703   | -0.0403  | —       | -0.3788   | -0.0803   | —        |
| (var. log <sub>e</sub> th) | (0.0997) | (0.2163)  | (0.1398) | —       | (0.1005)  | (0.0789)  | —        |
| r <sub>e</sub>             | 0.761    | 0.856     | 0.832    | —       | 0.854     | 0.682     | —        |
| α                          | 1.523    | 1.341     | 1.070    | —       | 0.9955    | 1.102     | —        |
| (var. α)                   | (0.0714) | (0.02288) | (0.0016) | —       | (0.01917) | (0.0812)  | —        |

TABLE 44. Statistics of the length (l) and thickness (th) of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 45

| n                          | A               | B               | C               | D               | E                | F               | G               |
|----------------------------|-----------------|-----------------|-----------------|-----------------|------------------|-----------------|-----------------|
| l mm.                      | 22              | 27              | 30              | 6               | 14               | 18              | 10              |
| (var. l)                   | 9.58<br>(1.994) | 8.57<br>(4.067) | 6.91<br>(9.460) | 8.47<br>(0.668) | 7.29<br>(13.003) | 7.17<br>(8.883) | 6.11<br>(7.806) |
| dl mm.                     | 2.33<br>(0.148) | 2.01<br>(0.214) | 1.78<br>(0.938) | 1.95<br>(0.108) | 1.71<br>(0.662)  | 1.72<br>(0.485) | 1.39<br>(0.576) |
| r.                         | 0.771           | 0.933           | 0.775           | 0.687           | 0.957            | 0.942           | 0.874           |
| a                          | 0.2724          | 0.2293          | 0.3148          | —               | 0.2256           | 0.2337          | 0.2717          |
| (var. a)                   | (0.00151)       | (0.00681)       | (0.0014)        | —               | (0.00035)        | (0.00038)       | (0.00218)       |
| log <sub>e</sub> l         | 2.2493          | 2.1215          | 1.7789          | —               | 1.8769           | 1.891           | 1.7151          |
| (var. log <sub>e</sub> l)  | (0.0217)        | (0.0536)        | (0.2013)        | —               | (0.2191)         | (0.1596)        | (0.1895)        |
| log <sub>e</sub> dl        | 0.8326          | 0.6722          | 0.4469          | —               | 0.4274           | 0.4663          | 0.1988          |
| (var. log <sub>e</sub> dl) | (0.0265)        | (0.0517)        | (0.2594)        | —               | (0.2037)         | (0.1519)        | (0.2610)        |
| r <sub>e</sub>             | 0.772           | 0.946           | 0.803           | —               | 0.98             | 0.964           | 0.886           |
| α                          | 1.105           | 0.9822          | 1.197           | —               | 0.9641           | 0.9756          | 1.175           |
| (var. α)                   | (0.02467)       | (0.00406)       | (0.01819)       | —               | (0.00307)        | (0.00421)       | (0.03707)       |

TABLE 45. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 46

|                            | A         | B         | C         | D      | E         | F         | G         |
|----------------------------|-----------|-----------|-----------|--------|-----------|-----------|-----------|
| n                          | 12        | 24        | 29        | 4      | 29        | 14        | 9         |
| l mm.                      | 9.93      | 7.31      | 7.57      | 8.75   | 5.9       | 7.54      | 5.97      |
| (var. l)                   | (2.191)   | (7.485)   | (3.593)   | (0.25) | (7.379)   | (10.149)  | (10.5)    |
| th mm.                     | 4.03      | 3.0       | 2.72      | 3.0    | 2.15      | 2.76      | 2.07      |
| (var. th)                  | (0.819)   | (1.646)   | (0.516)   | (1.18) | (0.844)   | (1.145)   | (0.828)   |
| r .                        | 0.725     | 0.926     | 0.699     | 0.3    | 0.958     | 0.902     | 0.891     |
| a                          | 0.6114    | 0.469     | 0.379     | —      | —         | 0.3359    | 0.2808    |
| (var. a)                   | (0.01773) | (0.00143) | (0.00271) | —      | —         | (0.00175) | (0.00233) |
| log <sub>e</sub> l         | 2.2837    | 1.9237    | 1.9936    | —      | 1.6777    | 1.9378    | 1.657     |
| (var. log <sub>e</sub> l)  | (0.0217)  | (0.131)   | (0.0612)  | —      | (0.1946)  | (0.1648)  | (0.2586)  |
| log <sub>e</sub> th        | 1.3689    | 1.0145    | 0.9667    | —      | 0.6819    | 0.9448    | 0.64      |
| (var. log <sub>e</sub> th) | (0.0498)  | (0.1681)  | (0.0677)  | —      | (0.1672)  | (0.1407)  | (0.1749)  |
| r <sub>e</sub>             | 0.718     | 0.93      | 0.698     | —      | 0.965     | 0.90      | 0.903     |
| α                          | 1.515     | 1.132     | 1.052     | —      | 0.9268    | 0.924     | 0.8224    |
| (var. α)                   | (0.1112)  | (0.00788) | (0.02102) | —      | (0.00219) | (0.01353) | (0.0178)  |

TABLE 46. Statistics of length (l) and maximum depth (th) of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 47

| n                         | A               | B              | C               | D              | E               | F              | G               |
|---------------------------|-----------------|----------------|-----------------|----------------|-----------------|----------------|-----------------|
| l mm.                     | 16              | 34             | 18              | 5              | 18              | 22             | 20              |
| (var. l)                  | 3.75<br>(0.439) | 3.07<br>(1.42) | 2.94<br>(1.947) | 3.4<br>(0.145) | 3.53<br>(1.683) | 3.52<br>(2.22) | 3.54<br>(1.957) |
| w mm.                     | 2.85            | 2.42           | 2.27            | 2.68           | 2.95            | 2.84           | 2.89            |
| (var. w)                  | (0.162)         | (0.526)        | (0.796)         | (0.166)        | (0.769)         | (0.932)        | (1.0)           |
| r.                        | 0.843           | 0.875          | 0.937           | -0.26          | 0.904           | 0.91           | 0.962           |
| a                         | 0.6076          | —              | —               | —              | —               | —              | —               |
| (var. a)                  | (0.00765)       | —              | —               | —              | —               | —              | —               |
| log <sub>e</sub> l        | 1.3068          | 1.0513         | 0.9765          | —              | 1.198           | 1.1761         | 1.1944          |
| (var. log <sub>e</sub> l) | (0.0306)        | (0.1407)       | (0.2037)        | —              | (0.1266)        | (0.1648)       | (0.145)         |
| log <sub>e</sub> w        | 1.0374          | 0.8402         | 0.7477          | —              | 1.0395          | 0.989          | 1.0046          |
| (var. log <sub>e</sub> w) | (0.0198)        | (0.0872)       | (0.1442)        | —              | (0.0846)        | (0.1096)       | (0.1133)        |
| r <sub>e</sub>            | 0.845           | 0.884          | 0.926           | —              | 0.922           | 0.91           | 0.981           |
| α                         | 0.8045          | 0.7873         | 0.8413          | —              | 0.8174          | 0.8155         | 0.8839          |
| (var. α)                  | (0.01323)       | (0.00424)      | (0.0063)        | —              | (0.00627)       | (0.005784)     | (0.00163)       |

TABLE 47. Statistics of length (l) and maximum width (w) of the ventral muscle scars of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 48

|                           | A         | B         | C         | D         | E        | F         | G         |
|---------------------------|-----------|-----------|-----------|-----------|----------|-----------|-----------|
| n.                        | 61        | 70        | 42        | 22        | 56       | 32        | 19        |
| l mm.                     | 7.13      | 7.08      | 6.57      | 7.44      | 5.81     | 7.48      | 6.21      |
| (var. l)                  | (3.794)   | (6.753)   | (6.16)    | (2.373)   | (8.733)  | (4.33)    | (4.286)   |
| c mm.                     | 1.47      | 1.49      | 1.47      | 1.45      | 1.28     | 1.6       | 1.41      |
| (var. c)                  | (0.158)   | (0.262)   | (0.279)   | (0.0766)  | (0.313)  | (0.184)   | (0.143)   |
| r.                        | 0.897     | 0.932     | 0.934     | 0.824     | 0.97     | 0.94      | 0.98      |
| a                         | 0.2041    | 0.197     | 0.2128    | 0.1796    | —        | 0.2061    | —         |
| (var. a)                  | (0.00014) | (0.00008) | (0.00014) | (0.00052) | —        | (0.00017) | —         |
| log <sub>e</sub> l        | 1.928     | 1.894     | 1.8157    | 1.9858    | 1.6444   | 1.975     | 1.7736    |
| (var. log <sub>e</sub> l) | (0.0725)  | (0.1266)  | (0.1336)  | (0.0421)  | (0.2303) | (0.0744)  | (0.10531) |
| log <sub>e</sub> c        | 0.35      | 0.3431    | 0.3247    | 0.3534    | 0.1594   | 0.4357    | 0.3097    |
| (var. log <sub>e</sub> c) | (0.0706)  | (0.1114)  | (0.1211)  | (0.0363)  | (0.1749) | (0.0686)  | (0.0677)  |
| r <sub>e</sub>            | 0.895     | 0.936     | 0.939     | 0.831     | 0.982    | 0.962     | 0.993     |
| α.                        | 0.9868    | 0.938     | 0.952     | 0.9285    | 0.8714   | 0.9602    | 0.8018    |
| (var. α)                  | (0.0033)  | (0.0016)  | (0.00269) | (0.01334) | (0.0005) | (0.00229) | (0.00529) |

TABLE 48. Statistics of length of brachial valve (l) and length of cardinalia (c) of n brachial valves of *Howellites antiquior* (M'Coy.) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B) *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 49

|                                 | A         | B         | C         | D         | E         | F         | G          |
|---------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|------------|
| n                               | 23        | 40        | 30        | 7         | 17        | 19        | 11         |
| $\bar{l}$ mm.                   | 9.51      | 8.2       | 7.46      | 8.26      | 7.91      | 6.97      | 7.55       |
| (var. l)                        | (2.012)   | (8.252)   | (7.065)   | (1.253)   | (9.606)   | (9.203)   | (5.846)    |
| $\bar{s}\bar{c}$ mm.            | 3.61      | 3.1       | 3.04      | 3.23      | 3.33      | 3.13      | 2.93       |
| (var. sc)                       | (0.404)   | (1.535)   | (1.414)   | (0.58)    | (1.894)   | (2.311)   | (1.129)    |
| $r$ .                           | 0.808     | 0.944     | 0.976     | 0.806     | 0.979     | 0.984     | 0.985      |
| a                               | 0.4481    | —         | —         | 0.6804    | 0.444     | 0.5011    | 0.4393     |
| (var. a)                        | (0.00332) | —         | —         | (0.03245) | (0.00055) | (0.00047) | (0.000641) |
| $\log_e \bar{l}$                | 2.2413    | 2.0455    | 1.9499    | 2.1021    | 1.9948    | 1.8549    | 1.973      |
| (var. $\log_e \bar{l}$ )        | (0.0217)  | (0.1159)  | (0.1194)  | (0.0185)  | (0.1442)  | (0.1733)  | (0.097)    |
| $\log_e \bar{s}\bar{c}$         | 1.2681    | 1.0572    | 1.0407    | 1.1452    | 1.124     | 1.0351    | 1.013      |
| (var. $\log_e \bar{s}\bar{c}$ ) | (0.0306)  | (0.1484)  | (0.1424)  | (0.0545)  | (0.1579)  | (0.2118)  | (0.1239)   |
| $r_e$                           | 0.806     | 0.945     | 0.991     | 0.835     | 0.967     | 0.995     | 0.985      |
| $\alpha$                        | 1.187     | 1.131     | 1.092     | 1.717     | 1.046     | 1.106     | 1.13       |
| (var. $\alpha$ )                | (0.00332) | (0.00361) | (0.00076) | (0.1784)  | (0.00474) | (0.00719) | (0.0041)   |

TABLE 49. Statistics of length of pedicle valve ( $\bar{l}$ ) and length of ventral muscle scar ( $\bar{s}\bar{c}$ ) of n pedicle valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 50

|                    | A         | B         | C         | D         | E         | F         | G         |
|--------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| n                  | 53        | 57        | 26        | 9         | 31        | 15        | 13        |
| $\bar{l}$ mm.      | 1.46      | 1.51      | 1.5       | 1.48      | 1.25      | 1.65      | 1.37      |
| (var. l)           | (0.14)    | (0.266)   | (0.25)    | (0.076)   | (0.385)   | (0.142)   | (0.139)   |
| $\bar{w}$ mm.      | 2.49      | 2.78      | 2.41      | 2.7       | 2.03      | 2.83      | 2.18      |
| (var. w)           | (0.434)   | (0.958)   | (0.69)    | (0.385)   | (1.193)   | (0.5493)  | (0.54)    |
| $\bar{r}$ .        | 0.849     | 0.939     | 0.953     | 0.621     | 0.959     | 0.906     | 0.845     |
| a                  | 1.761     | 1.898     | 1.661     | 2.246     | 1.761     | 1.967     | 1.969     |
| (var. a)           | (0.01697) | (0.00775) | (0.00106) | (0.44298) | (0.00858) | (0.05326) | (0.08806) |
| $\log_e \bar{l}$   | 0.3431    | 0.3568    | 0.3528    | 0.3748    | 0.1131    | 0.4754    | 0.279     |
| (var. $\log_e l$ ) | (0.064)   | (0.1105)  | (0.1053)  | (0.0344)  | (0.2199)  | (0.0507)  | (0.0715)  |
| $\log_e \bar{w}$   | 0.8793    | 0.9641    | 0.8235    | 0.9674    | 0.5809    | 1.0068    | 0.7253    |
| (var. $\log_e w$ ) | (0.0667)  | (0.1168)  | (0.1122)  | (0.0517)  | (0.2541)  | (0.0669)  | (0.1079)  |
| $\bar{r}_e$        | 0.863     | 0.939     | 0.96      | 0.628     | 0.974     | 0.903     | 0.857     |
| $\alpha$           | 1.021     | 1.028     | 1.033     | 1.226     | 1.075     | 1.149     | 1.229     |
| (var. $\alpha$ )   | (0.00521) | (0.00227) | (0.00348) | (0.13)    | (0.00205) | (0.01874) | (0.03637) |

TABLE 50. Statistics of length (l) and maximum width (w) of cardinalia of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



TABLE 5I

| n                          | A         | B         | C          | D         | E         | F         | G         |
|----------------------------|-----------|-----------|------------|-----------|-----------|-----------|-----------|
| ·                          | 62        | 68        | 31         | 22        | 40        | 32        | 17        |
| l mm.                      | 7·39      | 7·28      | 6·94       | 7·43      | 7·23      | 7·61      | 6·33      |
| (var. l)                   | (3·148)   | (6·131)   | (4·633)    | (2·42)    | (5·542)   | (4·408)   | (4·879)   |
| ad mm.                     | 4·09      | 3·95      | 3·92       | 3·95      | 3·93      | 4·14      | 3·73      |
| (var. ad)                  | (0·877)   | (1·617)   | (1·544)    | (0·756)   | (2·252)   | (1·533)   | (1·511)   |
| r.                         | 0·94      | 0·966     | 0·985      | 0·946     | 0·873     | 0·963     | 0·944     |
| a                          | 0·5279    | 0·5135    | 0·5774     | 0·5589    | —         | —         | 0·5565    |
| (var. a)                   | (0·00054) | (0·00027) | (0·000343) | (0·00164) | —         | —         | (0·00225) |
| log <sub>e</sub> l         | 1·9719    | 1·9303    | 1·8913     | 1·984     | 1·928     | 1·9928    | 1·8341    |
| (var. log <sub>e</sub> l)  | (0·0564)  | (0·1096)  | (0·0919)   | (0·043)   | (0·1005)  | (0·0734)  | (0·115)   |
| log <sub>e</sub> ad        | 1·3831    | 1·3243    | 1·318      | 1·3503    | 1·3005    | 1·3779    | 1·2642    |
| (var. log <sub>e</sub> ad) | (0·0507)  | (0·0988)  | (0·0962)   | (0·0468)  | (0·1362)  | (0·0856)  | (0·1044)  |
| r <sub>e</sub>             | 0·948     | 0·966     | 0·987      | 0·959     | 0·881     | 0·98      | 0·946     |
| α                          | 0·9481    | 0·9495    | 1·023      | 1·043     | 1·164     | 1·08      | 0·9528    |
| (var. α)                   | (0·00152) | (0·00092) | (0·00093)  | (0·00437) | (0·00799) | (0·00154) | (0·00683) |

TABLE 5I. Statistics of length of brachial valve (l) and length of adductor scar from umbo (ad) of n brachial valves of *Howellites antiquior* (M'Coy) from the Lower Longvillian, Meifod (A), *H. antiquior* (M'Coy) from the Gelli-grin Group, Bala (B), *H. ultima* Bancroft (C), *H. intermedia expectata* Bancroft (D), *H. intermedia* Bancroft (E), *H. striata lineata* Bancroft (F) and *H. striata* Bancroft (G).



|                                         | costellae per mm. |   |    |    |   |
|-----------------------------------------|-------------------|---|----|----|---|
|                                         | 2                 | 3 | 4  | 5  | 6 |
| <i>H. antiquior</i> (M'Coy) from Meifod | —                 | — | 8  | 3  | 1 |
| <i>H. antiquior</i> (M'Coy) from Bala   | —                 | — | 16 | 13 | 1 |
| <i>H. ultima</i> Bancroft               | —                 | 3 | 23 | 8  | — |
| <i>H. intermedia expectata</i> Bancroft | —                 | 1 | 7  | —  | — |
| <i>H. intermedia</i> Bancroft           | —                 | — | 14 | 7  | 2 |
| <i>H. striata lineata</i> Bancroft      | —                 | — | 12 | 8  | — |
| <i>H. striata</i> Bancroft              | —                 | — | 8  | 3  | 1 |

TABLE 52. The distribution of brachial valves of given species of *Howellites* with 2-6 costellae per mm., 5 mm. antero-medianly of the dorsal umbones.

TABLE 53

|                                         | 1 $\bar{a}\bar{1}$ ) 1 $\bar{b}$ | 2 $\bar{c}$ ) 2 $a^\circ$ | 3 $\bar{c}$ ) 3 $a^\circ$ | 4 $\bar{b}$ ) 4 $b^\circ$ | 4 $\bar{a}$ 1 $^\circ$ ) 4 $\bar{b}\bar{1}$ |
|-----------------------------------------|----------------------------------|---------------------------|---------------------------|---------------------------|---------------------------------------------|
| <i>H. antiquior</i> (M'Coy)—Meifod      | 5/7                              | 1/1                       | 9/10                      | 10/11                     | 0/2 (1)                                     |
| <i>H. antiquior</i> (M'Coy)—Bala        | 4/16                             | 9/9                       | 30/32 (2)                 | 21/22 (4)                 | 2/12                                        |
| <i>H. ultima</i> Bancroft               | 11/24 (2)                        | 13/20                     | 19/67 (4)                 | 29/64 (13)                | 17/23 (2)                                   |
| <i>H. cf. ultima</i> Bancroft           | 2/9 (1)                          | 0/5                       | 11/45 (2)                 | 27/44 (6)                 | 11/12 (1)                                   |
| <i>H. intermedia expectata</i> Bancroft | 0/1                              | 0/2                       | 6/8 (2)                   | 7/10 (1)                  | 0/5                                         |
| <i>H. intermedia</i> Bancroft           | 7/40 (7)                         | 25/33                     | 49/68                     | 38/48 (4)                 | 1/23 (1)                                    |
| <i>H. striata lineata</i> Bancroft      | 4/14 (3)                         | 8/10                      | 27/36                     | 25/31 (4)                 | 1/13 (2)                                    |
| <i>H. striata</i> Bancroft              | 1/10 (2)                         | 6/8                       | 23/32 (2)                 | 16/23 (6)                 | 3/11 (2)                                    |
| <i>H. cf. striata</i> Bancroft          | 4/10 (2)                         | 4/5                       | 21/28 (1)                 | 13/19 (7)                 | 1/11 (1)                                    |

TABLE 53. Proportions of brachial valves of given species of *Howellites* showing the earlier insertion of 5 costellae relative to 5 others (with the number of valves in which both costellae originated at the same growth stage in brackets).

### Genus *ONNIELLA* Bancroft 1928a

DIAGNOSIS (emended). Subcircular, gently and unequally biconvex dalmanellids with pedicle valve more deeply convex than sulcate brachial valve and evenly convex to subcarinate in transverse profile; radial ornamentation fascicostellate to multicostellate with externally branching costellae common in first four sectors of brachial valve; ventral interarea, short, curved, apsacline with open delthyrium and small umbo; dorsal interarea, short and curved, anacline, notothyrium commonly filled by cardinal process; shell punctate.

Ventral interior with strong or massive teeth supported by divergent dental lamellae, pedicle callist well developed, muscle field subpentagonal to widely cordate in outline with submedian diductor lobes extending beyond dental lamellae but rarely enclosing a narrow, lanceolate adductor scar; ventral pallial sinus pattern lemniscate with narrowly divergent *vascula media* branching well posterior of commissure.



Dorsal interior with undifferentiated bilobed cardinal process, commonly expanded into semi-ovoid structure, brachiophores with their bases greatly divergent relative to their tops, fulcral plates rarely developed ; dorsal adductor scars elongate with posterior elements either smaller than or about equal to anterior ones ; pallial sinus pattern not well known, probably lemniscate.

TYPE SPECIES. *Onniella broeggeri* Bancroft.

DISCUSSION. Bancroft (1928a : 55-57, 63-68) erected this genus with the intention of recognizing the characteristic profile of the shell and the degree of external branching in the first four sectors of the radial ornamentation on the brachial valve. Three new species were assigned to the genus, *O. broeggeri*, *O. reuschi* and *O. avelinei* and it is evident from his discussion of the last species (p. 57) that he considered it to be different from *O. broeggeri* only in details of outline and profile. Bancroft (1945 : 209-211) however, proposed another genus, *Soudleyella*, to embrace the type species, *S. soudleyensis* Bancroft and also *O. avelinei*. In his discussion of *Soudleyella* he made no direct comparison with *Onniella* although later (p. 215) he did remark that *Onniella* is " a large *Soudleyella*-like genus with a small ventral umbo, a large and complex cardinal process, widely divergent socket lines and a large anterior and small posterior scars in the dorsal valve ". But a small ventral umbo and widely divergent brachiophore bases (see Williams & Wright 1963 : 29) are also typical of *Soudleyella* while a complex cardinal process, which is known in gerontic shells of *Soudleyella*, is not invariably developed in species of *Onniella* and even Bancroft (1945 : 215) refers to " abnormal *Onniella* " with subequal adductor scars. In fact the two genera are inseparable morphologically and judging from textual emphasis on chronology, the real reason for Bancroft's reappraisal of his earlier systematic studies was probably the stratigraphical discontinuity between the species he assigned to *Soudleyella*, which were Harnagian and Soudleyan in age, and those he restricted to *Onniella* which ranged through the Marshbrookian, Actonian and Onnian. This use of time as a factor in taxonomic practice is a dangerous one. It ignores the effects of facies shifts, sorting of death assemblages and other controls governing the distribution of fossil remains and is not, at least for the present, a worthy substitute for morphological comparison.

***Onniella ostentata* sp. nov.**

(Pl. 7, figs. 3, 4, 7-11, 16)

DIAGNOSIS. Subcircular to subquadrate unequally biconvex *Onniella* with sulcate brachial valve about three-quarters as long as wide and about one-seventh as deep as long and evenly convex pedicle valve over one-quarter as deep as long ; radial ornamentation rather coarsely fascicostellate with modal count of 3 costellae per mm., 5 mm. anterior of dorsal umbo, external branching freely developed in sectors I to IV ; dental lamellae divergent, short, less than one-quarter as long as pedicle valve, teeth massive, crenulated ; adult ventral muscle field subpentagonal, less than two-fifths as long as pedicle valve and over four-fifths as wide as long with



submedian diductor lobes extending beyond but not enclosing lanceolate adductor scar ; cardinalia massive, less than one-fifth as long as brachial valve and less than one-half as long as wide, consisting of thick cardinal process commonly bilobed and filling entire notothyrium even in young growth stages and divergent brachio-phores so exaggerated by secondary shell deposition in adult shells as to form a solid transverse bar ankylosed with thickened median ridge, adductor scars, subquadrate with posterior and anterior elements subequal, divided by the median ridge and extending forward for over one-half the length of brachial valve.

|            |                                                                | length | width (mm.) |
|------------|----------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of brachial valve<br>(BB.29030)                 | 7.0    | 8.5         |
| PARATYPES. | External and internal mould of<br>brachial valve (BB.28932-33) | 10.0   | —           |
|            | Internal mould of brachial valve<br>(BB.28866)                 | —      | 4.7         |
|            | Internal and external mould of<br>brachial valve (BB.28868-69) | 8.0    | 9.5         |
|            | External mould of brachial valve<br>(BB.28867)                 | 8.0    | 10.0        |
|            | Internal mould of pedicle valve<br>(BB.28870)                  | 8.2    | —           |
|            | External mould of pedicle valve<br>(BB.28871)                  | 9.5    | —           |

HORIZON AND LOCALITIES. Gelli-grîn Group : BB.29030, BB.28870-71 from calcareous ash crags about 75 ft. south of the east end of ruined buildings in Ffridd Bach, south of Maes-meillion ; BB.28932-33, BB.28866 from calcareous ashes along the east side of the southern Rhiwlas Limestone outlier on Creigiau Bychain ; BB.28868-69 from calcareous ashes exposed at south end of wood, 850 ft. west of Gelli-grîn Farm ; BB.28867 from calcareous ashes exposed south of track, 1,900 ft. east-north-east of Bryn-briglas Farm.

***Onniella cf. soudleyensis* (Bancroft)**

(Pl. 7, figs. 12-15, 17, 18)

DESCRIPTION. Subcircular, unequally biconvex *Onniella* with a sulcate brachial valve about three-quarters as long as wide and about one-seventh as deep as long and subcarinate pedicle valve less than one-third as deep as long ; radial ornamentation fascicostellate with about 4 costellae per mm., 5 mm. anterior of the dorsal umbo ; external branching freely developed in sectors I to IV ; teeth strong, dental lamellae divergent, short just over one-fifth as long as the pedicle valve, ventral muscle field subpentagonal in adult valves extending anteriorly for less than two-fifths the length of the valve and over two-thirds as wide as long with the submedian diductor lobes extending forward of, but not enclosing, the lanceolate



adductor scar ; cardinal process strong, bilobed and crenulated posteriorly in adult valves but also thickening into a trilobed structure, brachiophores, strong, divergent, rarely flanked by fulcral plates, extending anteriorly for less than one-quarter the length of the brachial valve and over three-fifths as long as wide, dorsal adductor scars oval with anterior elements slightly larger than posterior ones, divided by a median ridge and extending anteriorly for nearly three-fifths the length of the brachial valve.

| MATERIAL (Figured).                            | length | width (mm.) |
|------------------------------------------------|--------|-------------|
| Internal mould of brachial valve<br>(BB.28874) | 9.5    | 11.0        |
| Internal mould of brachial valve<br>(BB.28873) | 3.0    | 3.8         |
| Internal mould of pedicle valve<br>(BB.28872)  | 9.0    | 9.5         |
| External mould of pedicle valve<br>(BB.28875)  | 7.5    | 8.5         |
| External mould of brachial valve<br>(BB.28876) | 11.2   | 12.5        |
| External mould of brachial valve<br>(BB.28877) | 3.5    | 5.0         |

HORIZON AND LOCALITY. Nant Hir Group : all specimens from mudstones exposed in left bank of Nant Hir, 600 ft. north-east of Cefn-y-maes Farm.

DISCUSSION. Two distinct forms of *Onniella* occurred in the Caradocian rocks of the Bala district, one from the Nant Hir Group, which compares with the description given by Bancroft (1945 : 210) for *S. soudleyensis* and may, provisionally at least, be referred to that species, and another from the Gelli-grŷn Group which is new.

Both stocks are alike in a number of attributes, including the outline of the brachial valve, the relative length of the dorsal adductor scars, the relative depth of the pedicle valve, and the relative lengths of the dental lamellae and the ventral muscle scar (Tables 55, 59, 60, 61, 63). Few data were obtained for some characters of *S. soudleyensis* but the mean percentage depth relative to length of six brachial valves was 15.3% (variance 7.25) which is not importantly different from the mean depth of the brachial valves of *O. ostentata* ; and although the mean percentage width relative to length of two ventral muscle scars, at 70, was 13 less than that for the muscle scars of *O. ostentata* (Table 62) larger samples of *S. soudleyensis* may show the difference to be insignificant. Similarly, although the small sample of ribbing associations in *S. soudleyensis* shows that the pattern is the same as that of *O. ostentata*, it is significantly finer ( $p < .01$ ). 2, 3, 4 and 5 costellae per mm. were counted 2 and 5 mm. respectively antero-medially of the dorsal umbones of 0, 2, 10, 3 and 1, 11, 3, 0 brachial valves of *O. ostentata*. Only two specimens of *S. soudleyensis* were sufficiently well preserved to give counts at the 5 mm. growth stage ; both were of 4 costellae per mm. At 2 mm., 4, 5, 6 and 7 costellae per mm. were noted in 1, 13, 3 and 3 specimens respectively.



But perhaps the most obvious difference ( $p < .01$ ) is in the development of the cardinalia which were consistently shorter relative to the length of the brachial valve and consistently wider relative to their own length in *O. ostentata*. These discrepancies resulted from the extravagant deposition of secondary shell substance around the brachioophores and cardinal process of *O. ostentata*, which was not simply a gerontic secretion as is shown by comparing the development of the cardinal process. In *S. soudleyensis*, the shaft, with or without a small posterior node representing the myophore, was exclusively characteristic of all growth stages of brachial valves up to 2 mm. long and occurred in 1 out of 5 valves between 3 and 4 mm. long. An enlarged bilobed myophore with a crenulated posterior face first appeared in 4 out of 11 valves 2 to 3 mm. long and persisted even in a valve 8 mm. long while a cardinal process, which was so enlarged that both myophore and shaft were entirely buried in secondary shell, did not occur in any valve less than 4.5 mm. long. In contrast, in the four youngest valves recovered of *O. ostentata*, which were all between 3–4 mm. long, the cardinal process was already a massive, semi-ovoid structure and the brachioophores cemented together to form a transverse bar.

TABLE 54

|                                                     | A             | B       | C   |
|-----------------------------------------------------|---------------|---------|-----|
| 1 $\bar{b}$ ) 1 $\bar{a}^\circ$                     | . . 2/6 (1)   | —       | 1/3 |
| 2 $\bar{b}$ ) 2 $\bar{a}^\circ$                     | . . 18/19 (1) | 4/4     | 3/3 |
| 2 $\bar{a}$ $\bar{I}$ ) 2 $\bar{b}$                 | . . 2/15 (2)  | 7/8 (1) | 1/1 |
| 3 $\bar{a}$ $\bar{I}$ $\bar{a}$ ) 3 $\bar{a}^\circ$ | . . 1/18      | 4/14    | 1/7 |
| 3 $\bar{a}$ $\bar{I}$ $\bar{a}$ ) 2 $\bar{a}^\circ$ | . . 1/3       | 9/9     | 1/1 |
| 3 $\bar{c}$ ) 3 $\bar{a}^\circ$                     | . . 1/18      | 1/14    | 1/7 |
| 3 $\bar{a}$ $\bar{I}^\circ$ ) 3 $\bar{b}$ $\bar{I}$ | . . 1/3       | 2/5     | —   |
| 4 $\bar{b}$ ) 4 $\bar{b}^\circ$                     | . . 0/12      | 1/17    | 0/2 |

TABLE 54. The proportions of the earlier insertion of 8 costellae relative to 8 others (with the number of valves in which both costellae originated at the same growth stage in brackets) for samples of *Onniella ostentata* sp. nov. (A), *O. broeggeri* Bancroft (B) and *O. cf. soudleyensis* (Bancroft) (C).

TABLE 55

|                | A                   | B                   |
|----------------|---------------------|---------------------|
| l mm. (var. l) | . . 4.76 (4.169).   | . . 3.44 (6.566)    |
| w mm. (var. w) | . . 6.34 (5.538).   | . . 4.66 (7.691)    |
| l              | . . 0.977           | . . 0.99            |
| a (var. a)     | . . 1.152 (0.00163) | . . 1.082 (0.00061) |

TABLE 55. Statistics of length (l) and maximum width (w) of 39 brachial valves of *Onniella ostentata* sp. nov. (A) and of 40 brachial valves of *O. cf. soudleyensis* (Bancroft) (B).



TABLE 56

|                  |   |   |        |           |
|------------------|---|---|--------|-----------|
| l mm. (var. l)   | . | . | 6.28   | (2.426)   |
| th mm. (var. th) | . | . | 0.96   | (0.116)   |
| r                | . | . | 0.467  |           |
| a (var. a)       | . | . | 0.2186 | (0.00235) |

TABLE 56. Statistics of length (l) and depth (th) of 18 brachial valves of *Onniella ostentata* sp. nov.

TABLE 57

|                |   | A      |           | B               |
|----------------|---|--------|-----------|-----------------|
| l mm. (var. l) | . | 7.3    | (1.998)   | 3.04 (2.766)    |
| c mm. (var. c) | . | 1.34   | (0.082)   | 0.7 (0.095)     |
| r              | . | 0.881  | .         | 0.945           |
| a (var. a)     | . | 0.2026 | (0.00036) | 0.1852 (0.0001) |

TABLE 57. Statistics of length of brachial valve (l) and length of cardinalia (c) of 28 specimens of *Onniella ostentata* sp. nov. (A) and 39 of *O. cf. soudleyensis* (Bancroft) (B).

TABLE 58

|                |   | A     |           | B                |
|----------------|---|-------|-----------|------------------|
| l mm. (var. l) | . | 1.31  | (0.099)   | 0.77 (0.141)     |
| w mm. (var. w) | . | 2.78  | (0.45)    | 1.26 (0.367)     |
| r              | . | 0.776 | .         | 0.958            |
| a (var. a)     | . | 2.132 | (0.07861) | 1.6134 (0.00738) |

TABLE 58. Statistics of length (l) and maximum width (w) of the cardinalia of 25 brachial valves of *Onniella ostentata* sp. nov. (A) and of 31 brachial valves of *O. cf. soudleyensis* (Bancroft) (B).

TABLE 59

|                  |   | A      |           | B                |
|------------------|---|--------|-----------|------------------|
| l mm. (var. l)   | . | 7.42   | (1.285)   | 3.72 (4.878)     |
| ad mm. (var. ad) | . | 3.88   | (0.506)   | 2.14 (1.04)      |
| r                | . | 0.813  | .         | 0.884            |
| a (var. a)       | . | 0.6275 | (0.00607) | 0.4617 (0.00258) |

TABLE 59. Statistics of length of brachial valve (l) and length of adductor scar from the umbo (ad) of 24 specimens of *Onniella ostentata* sp. nov. (A) and of 20 specimens of *O. cf. soudleyensis* (Bancroft) (B).

TABLE 60

|                  |   | A      |           | B                |
|------------------|---|--------|-----------|------------------|
| l mm. (var. l)   | . | 8.08   | (5.349)   | 4.7 (6.898)      |
| th mm. (var. th) | . | 2.18   | (0.378)   | 1.45 (0.644)     |
| r                | . | 0.72   | .         | 0.965            |
| a (var. a)       | . | 0.2658 | (0.00308) | 0.3056 (0.00043) |

TABLE 60. Statistics of length (l) and depth (th) of 13 pedicle valves of *Onniella ostentata* sp. nov. (A) and of 17 pedicle valves of *O. cf. soudleyensis* (Bancroft) (B).



TABLE 61

|                  |   |   | A      |           |   | B                |
|------------------|---|---|--------|-----------|---|------------------|
| l mm. (var. l)   | . | . | 7.94   | (6.051)   | . | 5.99 (7.288)     |
| sc mm. (var. sc) | . | . | 2.94   | (1.304)   | . | 2.23 (1.122)     |
| r                | . | . | 0.9    | .         | . | 0.966            |
| a (var. a)       | . | . | 0.4642 | (0.00274) | . | 0.3924 (0.00206) |

TABLE 61. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) of 17 specimens of *Onniella ostentata* sp. nov. (A) and of 7 specimens of *O. cf. soudleyensis* (Bancroft) (B).

TABLE 62

|                |   |   |        |           |
|----------------|---|---|--------|-----------|
| l mm. (var. l) | . | . | 2.88   | (1.194)   |
| w mm. (var. w) | . | . | 2.43   | (0.458)   |
| r              | . | . | 0.912  |           |
| a (var. a)     | . | . | 0.6194 | (0.00587) |

TABLE 62. Statistics of length (l) and maximum width (w) of ventral muscle scar of 13 specimens of *Onniella ostentata* sp. nov.

TABLE 63

|                  |   |   | A      |           | B                |
|------------------|---|---|--------|-----------|------------------|
| l mm. (var. l)   | . | . | 7.3    | (3.155)   | 4.48 (5.835)     |
| dl mm. (var. dl) | . | . | 1.74   | (0.212)   | 0.98 (0.29)      |
| r                | . | . | 0.968  | .         | 0.971            |
| a (var. a)       | . | . | 0.2592 | (0.00038) | 0.2229 (0.00021) |

TABLE 63. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) of 13 specimens of *Onniella ostentata* sp. nov. (A) and of 16 specimens of *O. cf. soudleyensis* (Bancroft) (B).

The massively developed cardinalia of *O. ostentata* distinguish it from the other species of *Onniella* described by Bancroft. In other characters it resembles *O. broeggeri* Bancroft but as can be seen from Table 54 the Gelli-grin shells also differed significantly ( $p < 0.01$ ) at least in the relatively early insertion of the costella 2 b.

### Genus **BANCROFTINA** Sinclair 1946

TYPE SPECIES. *Raymondella typa* Whittington by original designation of Sinclair (1946 : 295).

#### ***Bancroftina*** sp. (Pl. 7, figs. 19-23)

DESCRIPTION. Subcircular, unequally biconvex *Bancroftina* with a shield-shaped, gently convex, shallowly sulcate brachial valve about four-fifths as long as wide and a deeply and evenly convex pedicle valve, over two-fifths as deep as long with a short, curved, apsacline interarea ; radial ornamentation costellate with 2 or 3 costellae per mm. at 10 mm. antero-medially of the dorsal umbo, external branching rare ; ventral muscle scar bilobate, slightly longer than wide and extending forward for less than one-third the length of the valve ; cardinal process massive, fissured



and united with a strong high median ridge extending anteriorly for over half the length of the brachial valve and separating a pair of elongate adductor scars, brachiophores widely divergent, subtriangular in outline, sockets narrow, oblique.

| MATERIAL (Figured).                                               | length | width (mm.) |
|-------------------------------------------------------------------|--------|-------------|
| External mould of pedicle valve<br>(BB.29124)                     | —      | —           |
| Incomplete external moulds of<br>conjoined valves (BB.29148)      | 17.0   | —           |
| Internal mould of brachial valve<br>(BB.29149)                    | 17.0   | 17.0        |
| External and internal moulds of<br>conjoined valves (BB.29146-47) | 16.0   | 16.5        |

HORIZON AND LOCALITY. Gelli-grŷn Group : all specimens from the calcareous ashes above the Gelli-grŷn Limestone in the old quarries 1,800 ft. south of Bryn-melyn Farm.

DISCUSSION. Rare moulds of *Bancroftina* are known from the top calcareous ashes of the Gelli-grŷn Group and have been compared by Bancroft (1945 : 201) with *B. robusta*. The similarities, however, may prove not to be important because, although the outline of the ventral muscle field is like that of *B. robusta*, the radial ornamentation with the early insertion of  $2\bar{a}$  is more reminiscent of *B. typa* (Whittington) (see Bancroft 1945 : 198). In fact the differences between *B. typa* and *B. robusta*, like the larger size, the absence of "growth lines" and the shallow brachial valve etc. of the latter, are not necessarily significant and until comparative studies of these Shropshire forms together with larger collections of the Bala stock have been made, it would be misleading to attempt a specific identification of the Welsh specimens.

#### Family HARKNESSELLIDAE Bancroft 1928b

##### Genus *REUSCHELLA* Bancroft 1928b

TYPE SPECIES. *Reuschella semiglobata* Bancroft by original designation of Bancroft (1928b : 180).

##### *Reuschella* cf. *horderleyensis* Bancroft

(Pl. 8, figs. 1-10)

DESCRIPTION. Shell typically transversely subrectangular in outline but commonly modified by the early development of a pair of ears at the hinge-line so that the postero-lateral angles are acute, with relatively faster growth anterior of the hinge-line the postero-lateral angles become obtuse especially in adult shells, brachial valve about seven-tenths as long as wide, strongly and evenly convex on either side of the deep, angular median sulcus and about one-third as deep as long, but tending to flatten out laterally, pedicle valve unevenly convex, less than one-third as deep as long at the sharply angular median fold which, in adult valves, is flanked by a pair of shallow sulci passing laterally into a pair of shallow folds ; radial ornamentation fascicostellate with a modal count of 3 costellae per mm. in the



second sector, 10 mm. anterior of the dorsal umbo, externally branching costellae freely arising in sectors III and IV ; dental lamellae narrowly divergent, thin, extending forward for about one-fifth the length of the pedicle valve, teeth ridge-like, oblique to hinge-line ; pedicle callist small, ventral muscle field subtriangular to bilobed about four-fifths as wide as long with the submedian diductor lobes extending forward for over one-third the length of the pedicle valve but not enclosing the wide median adductor ; ventral pallial sinus pattern probably inequidistributate saccate ; crenulated myophore and shaft of adult brachial valves fused into elongately semi-oval structure commonly buttressed by low, ancillary struts, sockets, long, divergent and defined by fulcral plates extending laterally for just under twice the length of the narrowly divergent brachioophore bases which extend forward for about one-sixth the length of the brachial valve, crural pits small ; adductor pits deep with the anterior boundaries to the scars reaching forward of the dorsal umbo for less than one-half the length of the brachial valve ; dorsal pallial sinus pattern probably inequidistributate saccate.

**MATERIAL (Figured).**

|                                                                 | length | width (mm.) |
|-----------------------------------------------------------------|--------|-------------|
| Internal mould of conjoined valves<br>(BB.29132)                | 22.0   | —           |
| Internal and external moulds of<br>brachial valve (BB.28968-69) | 7.0    | 10.2        |
| Internal mould of pedicle valve<br>(BB.28970)                   | 4.2    | 7.0         |
| Internal mould of brachial valve<br>(BB.28971)                  | 17.0   | 23.0        |
| External mould of brachial valve<br>(BB.28972)                  | —      | —           |
| Internal mould of pedicle valve<br>(BB.28973)                   | 16.5   | 20.5        |
| Internal mould of brachial valve<br>(BB.28974)                  | 16.0   | 21.0        |
| External mould of pedicle valve<br>(BB.28975)                   | —      | —           |

**HORIZON AND LOCALITY.** Allt Ddu Group : all specimens from mudstones exposed on the western slopes of Coed Mawr, 1,200 ft. west-north-west of Rhiwlas House.

***Reuschella horderleyensis* Bancroft *undulata* subsp. nov.**

(Pl. 8, figs. 11-17)

**DIAGNOSIS.** Shell typically transversely subrectangular in outline but commonly modified by early development of ears at hinge line, acute postero-lateral angles later transformed to obtuse ones by faster growth of lateral commissure, brachial valve just over two-thirds as long as wide and evenly convex on either side of deep, angular median sulcus and over one-quarter as deep as long but tending to flatten laterally, pedicle valve over one-third as deep as long at sharply angular median fold, flanking submedian rounded sulci and complementary lateral folds well



developed ; radial ornamentation fascicostellate with modal count of 3 costellae per mm. in second sector, 10 mm. anterior of dorsal umbo, externally branching costellae freely arising in Sectors III and IV ; dental lamellae divergent, then, extending forward for about one-fifth of the length of pedicle valve, teeth strong, obliquely disposed to hinge line ; pedicle callist small, ventral muscle field sub-pentagonal to bilobed about four-fifths as wide as long with submedian diductor lobes extending forward for about one-third the length of pedicle valve but not enclosing wide, median adductor scar ; crenulated myophore and shaft of adult brachial valves fused into massive semi-oval to semi-circular structure, sockets long, divergent and defined by fulcral plates extending laterally for over one-half as much again as the length of narrowly divergent brachiophore bases which extend forward for about one-fifth the length of brachial valve, crural pits small ; adductor pits deep, anterior boundaries to adductor scars, poorly defined, reaching forward of dorsal umbo for about two-fifths the length of brachial valve.

|            |                                                                 | length | width (mm.) |
|------------|-----------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of pedicle valve<br>(BB.28860)                   | 16.0   | 21.0        |
| PARATYPES. | External and internal moulds of<br>brachial valve (BB.28861-62) | 12.0   | —           |
|            | External mould of pedicle valve<br>(BB.29031)                   | 17.0   | —           |
|            | External mould of pedicle valve<br>(BB.28863)                   | 21.0   | 29.0        |
|            | Internal mould of brachial valve<br>(BB.28864)                  | —      | —           |
|            | Internal mould of brachial valve<br>(BB.28865)                  | —      | —           |

HORIZON AND LOCALITIES. Gelli-grîn Group : BB.28860 from calcareous ashes exposed south of track, 1,900 ft. north-east of Bryn-briglas Farm ; BB.28861-62, BB.28865 from calcareous ash crags 40 ft. south of west end of ruined building in Ffridd Bach, south of Maes-meillion ; BB.29031 from calcareous ashes immediately west of fence at south-east end of prominent scarp of Rhiwlas Limestone, 500 ft. south-west of BM.1338.7, Bryn Pig ; BB.28863 from calcareous ashes above limestone in quarries east of fence, 650 ft. west-north-west of BM.1407.6, Bryn Pig ; BB.28864 from ashy mudstones in right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern Farm.

DISCUSSION. Anglo-Welsh species of *Reuschella* were segregated by Bancroft (1945 : 239) into two distinct groups typified by *R. bilobata* (J. de C. Sowerby) and *R. horderleyensis* Bancroft. The distinction between them was finely drawn, resting on the concave profile and independent lateral folds of the pedicle valve of the *R. bilobata* group and especially on the late insertion of costella 2a° in the brachial valves of the *R. horderleyensis* group. These differences are not taxonomically decisive because the Bala *Reuschella* are akin to *R. horderleyensis* in the pattern of radial ornamentation (Table 64), but also display variably developed lateral



folds as indeed do specimens of *R. horderleyensis* from the Llanyblodwel Beds (Whittington 1938a : 450) and even some shells of the closely related *R. oblonga* (Whittington 1938 : 252). This contradiction suggests that only ribbing can be effectively employed to distinguish between the two groups and that those Bala shells from the highest Allt Ddu mudstones and Gelli-grŷn ashes, which possess well developed lateral folds, are more appropriately compared with *R. horderleyensis* than *R. bilobata*.

The sample of *R. horderleyensis* obtained from the Llanyblodwel Beds was too small to use for comparisons of growth but in every respect of proportion for the characters listed in Tables 65-73 it did not differ from the older *Reuschella* found in the Bala district which may therefore be described, provisionally at least, as conspecific. The specimens making up this Bala sample were recovered from Lower Allt Ddu rocks where they are associated with *Dinorthis berwynensis* (Whittington) and *Heterorthis retrorsistria* (M'Coy). A few moulds, also comparable with *R. cf. horderleyensis* occur sporadically in the middle part of the Allt Ddu Group but the genus becomes quite common again in the highest Allt Ddu and the succeeding Gelli-grŷn Group, and when these specimens were compared with the older sample they were found to differ sufficiently to constitute a new subspecies.

Data essential to the comparison of the new subspecies with the older *Reuschella cf. horderleyensis* are set out in Tables 64-73. Only small numbers of brachial valves were well enough preserved to show details of radial ornamentation but it is evident that there is no difference between the two samples and the texture is also similar; 2 and 3 costellae per mm. were counted at a distance of 10 mm. anterior of the umbones of 3 and 7 brachial valves of *R. cf. horderleyensis* and 3 and 7 of the new subspecies respectively. Using length, width and depth for quantitative estimates of both the growth and residual proportions of shell outline and profile (Tables 65, 66) it was found that in such attributes the samples were alike, as they were too in the development of the lateral folds in the pedicle valves although those of the subspecies are better defined.

Internally, also, the samples were mainly so alike that they could have been drawn from the same population. The anterior boundary to the dorsal adductor field is commonly impressed in *Reuschella cf. horderleyensis*; it moved forward of the dorsal umbo at slightly less than one-half the increase in length of the brachial valve (Table 69). Such impressions were found in only two valves of the new subspecies but they were similarly proportioned. In both samples the anterior expansion of the dental lamellae (Table 73) and the relative width of the ventral muscle scar (Table 72) increased at a comparable rate and at the same time retained similar residual proportions; but in respect of the forward migration of the ventral muscle scars relative to the length of the pedicle valves, that of *R. cf. horderleyensis* was significantly faster ( $0.05 > p > 0.02$ ). Moreover, although the lateral growth of the fulcral plates did not differ significantly (Table 68) the brachiphore bases of the new subspecies were inherently larger than those of *R. cf. horderleyensis* but extended anteriorly relative to the length of the brachial valve at a significantly slower rate ( $0.05 > p > 0.02$ ). These statistics show that the cardinalia of younger



members of the *R. horderleyensis* "group" underwent an anterior shortening relative to their width in a manner recalling the increasing convergence of the "pre-socket lines" reported by Bancroft (1928 : 181) for the *R. bilobata* "group".

*Reuschella*, recovered from the highest Allt Ddu and succeeding Gelli-grn Groups, thus differs from *R. horderleyensis* in the relatively faster anterior expansion of both the supporting bases to the brachiophores and the ventral muscle field, which differences are worthy of subspecific recognition.

TABLE 64

|                                                         | A        | B        |
|---------------------------------------------------------|----------|----------|
| 2 $\bar{a}$ $\bar{I}$ 2 $a^\circ$ . .                   | 10/10    | 16/16    |
| 2 $\bar{b}$ ) 2 $a^\circ$ . .                           | 8/8      | 15/15    |
| 2 $\bar{b}$ $\bar{I}$ ) 2 $a^\circ$ . .                 | 1/1      | 6/6      |
| 2 $\bar{c}$ ) 2 $a^\circ$ . .                           | 2/2      | 8/8      |
| 3 $\bar{a}$ $\bar{I}$ ) 3 $a^\circ$ . .                 | 1/7 (4)  | 4/11 (1) |
| 3 $\bar{b}$ ) 3 $a^\circ$ . .                           | 1/11 (1) | 2/7 (2)  |
| 3 $\bar{c}$ ) 3 $b^\circ$ $\bar{I}^\circ$ . .           | 4/4      | —        |
| 4 $\bar{a}$ $\bar{I}$ ) 3 $b^\circ$ . .                 | 1/6 (2)  | 3/7      |
| 4 $\bar{a}$ $\bar{I}^\circ$ ) 4 $\bar{a}$ $\bar{I}$ . . | 1/7 (1)  | 2/3      |
| 4 $\bar{a}$ $\bar{I}^\circ$ ) 4 $\bar{b}$ . .           | 5/6      | 2/4      |

TABLE 64. The proportions of the earlier insertion of 10 costellae relative to 10 others (with the number of valves in which both costellae originated at the same growth stage in brackets) for samples of *Reuschella* cf. *horderleyensis* Bancroft (A) and *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 65

|                            | A               | B              |
|----------------------------|-----------------|----------------|
| $\bar{l}$ mm. (var. l) . . | 11.64 (20.401)  | 7.05 (10.975)  |
| $\bar{w}$ mm. (var. w) . . | 16.76 (39.667)  | 10.52 (22.092) |
| r . .                      | 0.989 . .       | 0.965          |
| a (var. a) . .             | 1.394 (0.00304) | 1.419 (0.0066) |

TABLE 65. Statistics of length (l) and maximum width (w) of 16 brachial valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and 23 brachial valves of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 66

|                                           | A               | B               |
|-------------------------------------------|-----------------|-----------------|
| $\bar{l}$ mm. (var. l) . .                | 13.27 (23.93)   | 11.66 (32.488)  |
| $\bar{th}$ mm. (var. th) . .              | 4.35 (3.931)    | 3.21 (2.563)    |
| r . .                                     | 0.91 . .        | 0.936           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . .   | 2.5219 (0.1272) | 2.349 (0.2142)  |
| $\log_e \bar{th}$ (var. $\log_e th$ ) . . | 1.3758 (0.1887) | 1.0551 (0.2223) |
| $r_e$ . .                                 | 0.931 . .       | 0.941           |
| $\alpha$ (var. $\alpha$ ) . .             | 1.218 (0.00988) | 1.019 (0.00516) |

TABLE 66. Statistics of length (l) and depth (th) of 22 brachial valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and 25 brachial valves of *Reuschella horderleyensis undulata* subsp. nov. (B).



TABLE 67

|                                           | A               | B               |
|-------------------------------------------|-----------------|-----------------|
| $\bar{l}$ mm. (var. l) . . .              | 14.68 (19.123)  | 12.54 (38.679)  |
| $\bar{c}$ mm. (var. c) . . .              | 2.53 (0.587)    | 2.60 (1.112)    |
| r . . .                                   | 0.932           | 0.92            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . . | 2.6437 (0.0856) | 2.4189 (0.2199) |
| $\log_e \bar{c}$ (var. $\log_e c$ ) . . . | 0.8841 (0.881)  | 0.8791 (0.1528) |
| $r_e$ . . .                               | 0.93            | 0.945           |
| $\alpha$ (var. $\alpha$ ) . . .           | 1.014 (0.00397) | 0.8336 (0.0031) |

TABLE 67. Statistics of length of brachial valve (l) and length of cardinalia (c) for 37 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A), and 26 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 68

|                                           | A                | B               |
|-------------------------------------------|------------------|-----------------|
| $\bar{l}$ mm. (var. l) . . .              | 2.6 (0.589)      | 2.57 (1.13)     |
| $\bar{w}$ mm. (var. w) . . .              | 4.86 (1.251)     | 4.14 (3.19)     |
| r . . .                                   | 0.809            | 0.911           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . . | 0.9358 (0.0837)  | 0.8649 (0.1579) |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . . . | 1.5551 (0.0517)  | 1.3553 (0.1707) |
| $r_e$ . . .                               | 0.829            | 0.904           |
| $\alpha$ (var. $\alpha$ ) . . .           | 0.7859 (0.00841) | 1.039 (0.00823) |

TABLE 68. Statistics of length (l) and maximum width (w) of cardinalia of 25 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A) and 26 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 69

|                                |                 |
|--------------------------------|-----------------|
| $\bar{l}$ mm. (var. l) . . .   | 15.39 (15.362)  |
| $\bar{sc}$ mm. (var. sc) . . . | 7.48 (3.174)    |
| r . . .                        | 0.942           |
| a (var. a) . . .               | 0.4546 (0.0013) |

TABLE 69. Statistics of length of brachial valve (l) and length of adductor scar (sc) for 20 specimens of *Reuschella* cf. *horderleyensis* Bancroft.

TABLE 70

|                                | A                | B                |
|--------------------------------|------------------|------------------|
| $\bar{l}$ mm. (var. l) . . .   | 13.9 (13.538)    | 11.48 (33.636)   |
| $\bar{th}$ mm. (var. th) . . . | 4.25 (1.058)     | 4.01 (3.394)     |
| r . . .                        | 0.836            | 0.916            |
| a (var. a) . . .               | 0.2796 (0.00214) | 0.3176 (0.00108) |

TABLE 70. Statistics of length (l) and thickness (th) of 13 pedicle valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and of 17 pedicle valves of *Reuschella horderleyensis undulata* subsp. nov. (B).



TABLE 71

|                                      | A      |           | B      |           |
|--------------------------------------|--------|-----------|--------|-----------|
| $\bar{l}$ mm. (var. l) . . .         | 14.63  | (22.351)  | 14.5   | (31.702)  |
| $\bar{s}\bar{c}$ mm. (var. sc) . . . | 5.38   | (4.206)   | 4.9    | (3.932)   |
| $\bar{r}$ . . .                      | 0.92   |           | 0.972  |           |
| $\alpha$ (var. $\alpha$ ) . . .      | 0.4338 | (0.00111) | 0.3521 | (0.00038) |

TABLE 71. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 28 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A) and for 21 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 72

|                                           | A      |           | B      |           |
|-------------------------------------------|--------|-----------|--------|-----------|
| $\bar{l}$ mm. (var. l) . . .              | 5.7    | (4.445)   | 4.88   | (3.756)   |
| $\bar{w}$ mm. (var. w) . . .              | 4.67   | (1.544)   | 3.93   | (1.804)   |
| $\bar{r}$ . . .                           | 0.913  |           | 0.906  |           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . . | 1.6764 | (0.1283)  | 1.5117 | (0.1468)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . . . | 1.5068 | (0.0687)  | 1.313  | (0.1105)  |
| $\bar{r}_e$ . . .                         | 0.929  |           | 0.917  |           |
| $\alpha$ (var. $\alpha$ ) . . .           | 0.7317 | (0.00367) | 0.8676 | (0.00665) |

TABLE 72. Statistics of length (l) and maximum width (w) of ventral muscle scars of 22 pedicle valves of *Reuschella* cf. *horderleyensis* Bancroft (A) and of 20 pedicle valves of *Reuschella horderleyensis undulata* subsp. nov. (B).

TABLE 73

|                                                   | A      |           | B      |           |
|---------------------------------------------------|--------|-----------|--------|-----------|
| $\bar{l}$ mm. (var. l) . . .                      | 14.23  | (20.283)  | 15.65  | (35.826)  |
| $\bar{d}\bar{l}$ mm. (var. dl) . . .              | 2.98   | (0.887)   | 3.15   | (1.759)   |
| $\bar{r}$ . . .                                   | 0.84   |           | 0.914  |           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . .         | 2.6077 | (0.0953)  | 2.6825 | (0.1362)  |
| $\log_e \bar{d}\bar{l}$ (var. $\log_e dl$ ) . . . | 1.0442 | (0.0953)  | 1.0658 | (0.1631)  |
| $\bar{r}_e$ . . .                                 | 0.868  |           | 0.909  |           |
| $\alpha$ (var. $\alpha$ ) . . .                   | 1.0    | (0.00797) | 1.095  | (0.01096) |

TABLE 73. Statistics of length of pedicle valve (l) and length of dental lamellae (dl) for 33 specimens of *Reuschella* cf. *horderleyensis* Bancroft (A) and for 21 specimens of *Reuschella horderleyensis undulata* subsp. nov. (B).

Family HETERORTHIDAE Schuchert & Cooper 1931

Genus **HETERORTHIS** Hall & Clarke 1892

TYPE SPECIES. *Orthis clytie* Hall by original designation of Hall & Clarke (1892 : 409).



*Heterorthis alternata* (J. de C. Sowerby)

(Pl. 9, figs. 1-6, 8, 9)

1839 *Orthis alternata* J. de C. Sowerby : 638, pl. 19, fig. 6.1871 *Orthis alternata* J. de C. Sowerby ; Davidson : 264, pl. 31, figs. 1-8.

DIAGNOSIS. Subcircular, plano- to concavo-convex *Heterorthis* with gently and evenly convex pedicle valve about one-sixth as deep as long and a brachial valve, commonly plane, about seven-tenths as long as wide, radial ornamentation finely costellate, commonly 3-4 ribs per mm., 10 mm. anterior of umbo, costellae sporadically accentuated ; ventral interarea apsacline with narrow, open delthyrium, dorsal interarea shorter, anacline with angular chilidium covering postero-dorsal surface of cardinal process ; ventral muscle field flabellate, more than two-thirds as long as pedicle valve and slightly broader than long, consisting of pair of semi-oval adjustor scars, disposed posteriorly of diductors, on either side of small pedicle callist, heart-shaped pair of adductor impressions extending forward of umbo for about three-tenths the length of valve, and pair of large diductor scars, including two divergent submedian lobes separated at their tips by a distance over two-fifths the length of valve and pair of smaller, semi-oval, lateral lobes ; ventral pallial sinus pattern probably lemniscate ; cardinal process, high, narrow, rarely encased in massive secondary deposits, ancillary ridges low when present, brachiophores simple, narrowly divergent with bases extending anteriorly for over one-seventh the length of valve ; dorsal adductor field oval, quadripartite deeply impressed especially posteriorly and extending anterior of umbo for over two-fifths the length of valve ; dorsal pallial sinus lemniscate ; subperipheral rims developed in interiors of both adult valves.

## MATERIAL (Figured).

|                                                           | length | width (mm.) |
|-----------------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.28901)             | 23.0   | 29.0        |
| External mould of pedicle valve<br>(BB.29134)             | 21.0   | —           |
| External mould of brachial valve<br>(BB.28903)            | 24.0   | 32.0        |
| Internal mould of brachial valve<br>(BB.28904)            | 18.0   | 24.0        |
| Internal mould of pedicle valve<br>(BB.28905)             | 22.0   | 28.0        |
| Internal mould of brachial valve<br>(BB.28906)            | 22.5   | 26.0        |
| Incomplete internal mould of<br>pedicle valve (BB.28907)  | —      | —           |
| Incomplete internal mould of<br>brachial valve (BB.28902) | 7.0    | —           |

HORIZON AND LOCALITY. Upper Longvillian Substage : all specimens from the Alternata Limestone exposed at Soudley Quarry, 2 miles south-east of Church Stretton, Shropshire.



***Heterorthis* cf. *retrorsistria* (M'Coy)**

(Pl. 9, figs. 7, 10-17)

1852 *Orthis retrorsistria* M'Coy : 224, pl. 1H, figs. 12, 13.1871 *Orthis alternata* Sow. var. *retrorsistria* M'Coy ; Davidson : 265, pl. 36, figs. 39-42.

DIAGNOSIS. Subcircular, gently convexo- to concavo-convex *Heterorthis* with an evenly convex pedicle valve less than one-third as deep as long and brachial valve, more commonly flat, less than three-quarters as long as wide and rarely faintly sulcate antero-medianly ; radial ornamentation finely costellate, commonly 4 ribs per mm., 10 mm. anterior of umbo, costellae sporadically thickened ; ventral interarea apsacline with narrow, open delthyrium, dorsal interarea shorter, anacline with subangular chilidium covering postero-dorsal surface of cardinal process ; ventral muscle field variable, flabellate, about two-thirds as long as pedicle valve and about four-fifths as wide as long, including an oval to cordate pair of adductor scars commonly deeply impressed and extending anterior of umbo for about three-tenths the length of valve, submedian diductor lobes wide, separated at their anterior tips by a distance nearly one-half the length of valve, lateral diductor lobes narrow, strip-like, adjustors obscure, pedicle callist well-defined ; ventral pallial sinus probably lemniscate ; cardinal process of adult valves, massive, semi-ovoid commonly ankylosed to high ancillary buttresses, brachioophores simple divergent with bases extending anteriorly for about one-sixth the length of valve ; dorsal adductor scars, oval and quadripartite, deeply impressed especially posteriorly and extending anterior of umbo for nearly one-half the length of valve ; dorsal pallial sinus lemniscate ; subperipheral rims developed in interiors of both adult valves.

## MATERIAL (Figured).

|                                                | length | width (mm.) |
|------------------------------------------------|--------|-------------|
| Internal mould of brachial valve<br>(BB.28908) | 15.5   | 21.5        |
| External mould of brachial valve<br>(BB.28909) | 16.5   | —           |
| Internal mould of pedicle valve<br>(BB.28910)  | 7.5    | 9.5         |
| External mould of brachial valve<br>(BB.28911) | —      | —           |
| External mould of pedicle valve<br>(BB.28912)  | —      | 16.5        |
| External mould of brachial valve<br>(BB.28913) | 16.0   | 21.0        |
| Internal mould of pedicle valve<br>(BB.28914)  | 14.0   | 18.0        |
| Internal mould of brachial valve<br>(BB.28916) | 7.2    | —           |
| Internal mould of brachial valve<br>(BB.28954) | 3.0    | 4.8         |



HORIZON AND LOCALITY. Allt Ddu Group: all specimens from mudstones exposed on the western slopes of Coed Mawr, 1,200 ft. west-north-west of Rhiwlas House.

DISCUSSION. Since the publication of M'Coy's description of *Heterorthis retrorsistria* (M'Coy 1852) there have been some misgivings on the validity of this species. Davidson (1871: 265), followed Salter, in believing the stock to be a small variety of *H. alternata* and simply reported without comment M'Coy's contention that the "backward curving of the lateral striae to terminate on the hinge-line" was systematically important. As Bancroft (1945: 239) pointed out this is not a reliable feature exclusive to *H. retrorsistria* and since heterorthids, morphologically indistinguishable from the type specimens of *H. retrorsistria*, occur abundantly in the Lower Allt Ddu, a sample of them has been compared with one of *H. alternata* from the Upper Longvillian of Shropshire.

Data on shell shape and profile are given in Tables 74-81 and they show that the brachial valves of both species were affected by allometry, but that *H. retrorsistria* grew longer, relative to width, faster than *H. alternata* and a comparison of the growth axes,  $\alpha$ , showed that the difference is significant ( $p < .01$ ). The pedicle valves of *H. retrorsistria* are also more strongly convex than those of *H. alternata* due not to any acceleration in growth rate, but to an inherently greater depth of the valve for the indices of inherent shape,  $b$ , were significantly different at the 5% level. The differences in the profiles of the brachial valves are more difficult to assess contrary to the assertion of Bancroft (1945: 239). In both samples the valves may be planar, slightly convex or gently concave although the last condition was usually a late growth modification of a juvenile planar attitude. These three profiles were displayed respectively by 11, 15 and 16 valves of *H. retrorsistria* and by 1, 21 and 3 valves of *H. alternata* so that although those of the former were more variable in convexity, planar valves were commonest in both samples. The same caution must also be exercised over the use of radial ornamentation for specific diagnosis. The pattern is fundamentally the same in both samples but at 10 mm. anterior of the dorsal umbones, counts of 3, 4 and 5 costellae per mm. were obtained in 4, 21 and 15 specimens of *H. retrorsistria* and 7, 8 and 1 of *H. alternata* respectively showing that the ribbing of *H. retrorsistria* tended to be finer but not significantly so.

Internally, differences occur in both valves. The ventral muscle field of *Heterorthis* is highly characteristic and in respect of relative dimensions there are no important differences between the two species either in differential growth or in indices of residual shape (Tables 78-81). Thus the muscle fields of both samples are comparable in their maximum widths relative to their maximum lengths but this statistical similarity conceals a fundamental contrast in the disposition of their constituents. In *H. alternata*, the submedian diductor lobes are narrow, parallel-sided impressions and the maximum width of the entire field is increased by the distension of the lateral lobes as a pair of flanking, semi-oval indentations. In *H. retrorsistria* the lateral lobes are very much reduced and the maximum width is subtended between the lateral edges of the submedian lobes which are splayed out antero-laterally.



TABLE 74

|                                           | A                | B                |
|-------------------------------------------|------------------|------------------|
| $\bar{l}$ mm. (var. l) . . .              | 8.92 (21.265)    | 11.89 (36.719)   |
| $\bar{w}$ mm. (var. w) . . .              | 12.43 (37.155)   | 16.95 (57.655)   |
| $r$ . . .                                 | 0.986 . . .      | 0.986            |
| $\log_e \bar{l}$ (var. $\log_e l$ ) . . . | 2.0699 (0.2367)  | 2.3592 (0.2311)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) . . . | 2.4126 (0.2151)  | 2.7387 (0.1831)  |
| $r_e$ . . .                               | 0.996 . . .      | 0.994            |
| $\alpha$ (var. $\alpha$ ) . . .           | 0.9534 (0.00013) | 0.8901 (0.00026) |

TABLE 74. Statistics of the length ( $l$ ) and maximum width ( $w$ ) of 59 brachial valves of *Heterorthis retrorsistria* (M'Coy) (A) and 38 brachial valves of *H. alternata* (J. de C. Sowerby) (B).

TABLE 75

|                                | A               | B                |
|--------------------------------|-----------------|------------------|
| $\bar{l}$ mm. (var. l) . . .   | 13.92 (7.312)   | 17.46 (32.314)   |
| $\bar{sc}$ mm. (var. sc) . . . | 6.4 (1.74)      | 7.63 (7.813)     |
| $r$ . . .                      | 0.929 . . .     | 0.803            |
| $a$ (var. $a$ ) . . .          | 0.4879 (0.0009) | 0.4917 (0.00277) |

TABLE 75. Statistics of the length of brachial valves ( $l$ ) and length of the adductor scars measured from the umbones ( $sc$ ) for 38 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and 33 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 76

|                              | A                | B               |
|------------------------------|------------------|-----------------|
| $\bar{l}$ mm. (var. l) . . . | 13.17 (11.754)   | 17.52 (33.251)  |
| $\bar{c}$ mm. (var. c) . . . | 2.05 (0.404)     | 2.51 (0.809)    |
| $r$ . . .                    | 0.832 . . .      | 0.825           |
| $a$ (var. $a$ ) . . .        | 0.1854 (0.00028) | 0.156 (0.00026) |

TABLE 76. Statistics of the length of brachial valves ( $l$ ) and length of cardinalia ( $c$ ) for 41 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and 32 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 77

|                                | A                | B               |
|--------------------------------|------------------|-----------------|
| $\bar{l}$ mm. (var. l) . . .   | 12.54 (14.134)   | 17.58 (27.062)  |
| $\bar{th}$ mm. (var. th) . . . | 3.75 (1.53)      | 3.00 (0.764)    |
| $r$ . . .                      | 0.786 . . .      | 0.76            |
| $a$ (var. $a$ ) . . .          | 0.3289 (0.00172) | 0.168 (0.00596) |

TABLE 77. Statistics of the length ( $l$ ) and thickness ( $th$ ) of 26 pedicle valves of *Heterorthis retrorsistria* (M'Coy) (A) and of 22 pedicle valves of *H. alternata* (J. de C. Sowerby) (B).



TABLE 78

|                        | A                | B                |
|------------------------|------------------|------------------|
| l mm. (var. l) . . .   | 13.98 (8.43).    | 20.68 (13.859)   |
| sc mm. (var. sc) . . . | 9.25 (5.681)     | 14.07 (7.525)    |
| r . . . . .            | 0.926 . . . . .  | 0.958            |
| a (var. a) . . . . .   | 0.8209 (0.00282) | 0.7368 (0.00235) |

TABLE 78. Statistics of the length of pedicle valves (l) and length of the ventral muscle field measured from the umbo (sc) for 36 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and 36 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 79

|                      | A                | B                |
|----------------------|------------------|------------------|
| l mm. (var. l) . . . | 10.04 (3.166)    | 14.37 (7.871)    |
| w mm. (var. w) . . . | 8.74 (2.688)     | 14.52 (7.190)    |
| r . . . . .          | 0.889 . . . . .  | 0.956            |
| a (var. a) . . . . . | 0.9214 (0.01114) | 0.9558 (0.00394) |

TABLE 79. Statistics of the length (l) and maximum width (w) of the ventral muscle field of 18 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and of 22 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 80

|                        | A                | B                |
|------------------------|------------------|------------------|
| l mm. (var. l) . . .   | 14.97 (3.768)    | 21.25 (15.089)   |
| ad mm. (var. ad) . . . | 4.43 (0.483)     | 6.33 (1.995)     |
| r . . . . .            | 0.667 . . . . .  | 0.819            |
| a (var. a) . . . . .   | 0.3581 (0.00339) | 0.3636 (0.00336) |

TABLE 80. Statistics of the length of pedicle valves (l) and length of the adductor scars measured from the umbones (ad) of 23 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and of 15 of *H. alternata* (J. de C. Sowerby) (B).

TABLE 81

|                        | A                | B                |
|------------------------|------------------|------------------|
| l mm. (var. l) . . .   | 9.83 (2.86).     | 14.39 (6.764)    |
| di mm. (var. di) . . . | 4.61 (0.981)     | 6.23 (1.259)     |
| r . . . . .            | 0.377 . . . . .  | 0.563            |
| a (var. a) . . . . .   | 0.5857 (0.01398) | 0.4314 (0.06359) |

TABLE 81. Statistics of the length (l) and anterior separation (di) of the ventral diductor scars of 23 specimens of *Heterorthis retrorsistria* (M'Coy) (A) and of 22 of *H. alternata* (J. de C. Sowerby) (B).

The extensions, anterior of the umbo, of both the brachiophore bases and the deeply impressed adductor scars relative to the length of the brachial valves are again similar in growth and inherent shape (Tables 75, 76). Indeed the dorsal interiors are very much alike in all details except for the form of the cardinal process. In young brachial valves of both species up to about 10 mm. long, the cardinal process is a simple, median plate, subtriangular in outline, with a flattened posterior surface covered dorsally by the chilidium and commonly pointed ventrally. In



*H. alternata*, the plate stands high above the notothyrial platform and remained so during subsequent growth although the cardinal process itself may have been thickened especially along its ventral surface and in 2 out of 24 specimens out-growths from the notothyrial platform formed a pair of low flanking buttresses to the cardinal process. In *H. retrorsistria*, these ancillary buttresses were already strongly developed even in valves less than 10 mm. long, where they enveloped the anterior surfaces of the cardinal process. In adult valves they stood only slightly lower than the median plate so that with the excessive thickening that occurred, the entire structure filled the notothyrium as a massive, semi-ovoid, trilobed receptacle for the diductor bases. This pattern seems to have been almost invariable: in only 1 out of 23 adult valves were the ancillary buttresses poorly developed although the median plate was very much thickened and semi-ovoid in ventral outline.

Despite many similarities then, *H. retrorsistria* differs from *H. alternata* in the relatively faster growth in length of the brachial valve, the more highly convex pedicle valve, the small size of the lateral lobes and the splayed ends of the submedian lobes making up the diductor scars and also in the large trilobed cardinal process which fills the notothyrium of adult brachial valves.

#### Family LINOPORELLIDAE Schuchert & Cooper 1931

##### Genus *SALOPIA* Williams 1955

TYPE SPECIES. *Orthis salteri* Davidson by original designation of Williams (*In* Whittington & Williams 1955 : 409)

##### *Salopia* sp

(Pl. 10, figs. 1, 2)

An internal mould of a brachial valve (BB.28915) 6.0 mm. long, 7.5 mm. wide and 2.3 mm. high, has been recovered from calcareous ashes of the Gelli-grîn Group exposed at the south edge of the wood, 850 ft. west of Gelli-grîn Farm. The valve was evidently subcircular in outline, with a short, anacline interarea medianly about one-seventh as long as the valve, and evenly convex in profile with a shallow median sulcus. Judging from the margin of the mould, the surface of the valve was finely multicostellate so that 4 costellae per mm. crenulated the antero-median part of the commissure. The cardinalia consisted of a thin blade-like cardinal process, a pair of strong, divergent brachiophores rectangular in outline and ankylosed to a pair of small fulcral plates that defined semi-ovoid sockets and to a pair of short brachiophore bases which converged on to the median septum at about one-quarter the length of the valve anterior of the umbo. The septum, which stood at mid-point about 0.5 mm. above the valve floor, was narrow and reached almost to the anterior margin. The adductor scars were impressed on either side of the septum, just anterior of the brachiophore bases, as a pair of narrow indentations, extending anteriorly for three-quarters the length of the valve and were divided by narrowly divergent *vascula myaria* into a smaller postero-lateral pair and a larger, subtriangular antero-median pair.



The valve is undoubtedly related to *Salopia salteri* and its subspecies *S. salteri gracilis* (see Whittington & Williams 1955 : 410-411) but it may ultimately prove to belong to a distinct stock with a more strongly convex brachial valve and a better defined median septum.

Superfamily TRIPLESIIACEA Quenstedt 1931

Family TRIPLESIIDAE Quenstedt 1931

Genus **BICUSPINA** Havlíček 1950

TYPE SPECIES. *Orthis cava* Barrande by original designation of Havlíček (1950 : 87).

***Bicuspina spiriferoides*** (M'Coy)

(Pl. 10, figs. 3-10)

1851 *Strophomena spiriferoides* M'Coy : 402.

1852 *Leptaena (Strophomena) spiriferoides* (M'Coy) M'Coy : 246.

1871 *Orthis ? spiriferoides* (M'Coy) Davidson : 275, pl. 37, figs. 3-7.

DIAGNOSIS (emended). Subquadrate, unequally biconvex *Bicuspina*, hinge-line wide, cardinal angles rectangular or rarely slightly obtuse ; pedicle valve less than one-half as deep as long, ventral sulcus persistent throughout growth, deep and tending to be flat-bottomed with parallel sides, just over one-third as wide as long ; brachial valve just over two-thirds as long as wide and over one-half as deep as long with high, median, flat-topped, parallel-sided fold ; ventral interarea curved, apsacline, pseudodeltidium folded into narrow arch medianly, dorsal interarea obsolete ; radial ornamentation consisting of fine costellae, rounded in transverse profile, having wavelength of about 0.5 mm. and arising either by branching or intercalation from up to 11 primary costae on either flank and 3 in sulcus ; concentric ornamentation very finely developed, consisting of about 7 lamellae per mm., about 10 mm. anterior of umbo ; pedicle tube slightly curved, just over one-quarter as long as pedicle valve, teeth well developed, pointed, supported by long, slightly divergent dental lamellae extending anteriorly for about one-third the length of valve along its floor and tending to become obscured in adult shells by excessive secondary shell secretion ; ventral muscle field extending forward of ventral umbo for nearly two-thirds the length of pedicle valve and consisting of pair of broad, semi-oval, centrally-placed adductor scars and pair of subtriangular, diductor scars extending well forward of adductors but not enclosing them ; ventral pallial sinus pattern vaguely impressed, possibly lemniscate, *vascula media* subjacent, arising from anterior end of diductor scars ; cardinal process bilobed with long basal shaft curving posteriorly, saddle small, sockets oblique, widely splayed brachiphores subtriangular and blade-like and disposed subparallel with hinge-line, dorsal adductor scars quadripartite impressed mainly on flanks of fold and segregated by faint low median ridge and normal to it, a pair of strong curved ridges representing traces of *vascula myaria*, anterior adductors subtriangular, about equal in size to subrectangular posterior pair and extending forward of dorsal umbo for over two-fifths the length of valve ; pallial sinus pattern obscure.



|            |                                                                             | length | width (mm.) |
|------------|-----------------------------------------------------------------------------|--------|-------------|
| LECTOTYPE. | Internal mould of brachial valve<br>(A.42457a)                              | 13.0   | 23.0        |
|            | External mould of incomplete<br>crushed shell (dorsal aspect)<br>(A.42457b) | —      | —           |
|            | Incomplete external mould of<br>pedicle valve (A.42457c)                    | —      | —           |
|            | OTHER<br>MATERIAL                                                           |        |             |
|            | Incomplete internal mould of<br>pedicle valve (A.42458)                     | 12.5   | —           |
|            | Incomplete external mould of<br>brachial valve (BB.29032)                   | —      | —           |
|            | Incomplete external mould of<br>pedicle valve (BB.29033)                    | —      | —           |
|            | Incomplete internal mould of<br>pedicle valve (BB.29034)                    | 18.0   | —           |

HORIZON AND LOCALITIES. Gelli-grŷn Group: lectotypes A.42457-58 from "Limestone schists of Bala"; BB.29033 from calcareous ash crags 75 ft. south of east end of ruined building in Ffridd Bach, south of Maes-meillion; BB.29034 from calcareous ashes exposed in field 300 ft. south of Y Garnedd Farm; BB.29032 from calcareous ash crags cropping out just west of a fence 1,100 ft., almost due west of Gelli-grŷn Farm.

DISCUSSION. One of the most distinctive brachiopods found in the Caradocian rocks of south Britain is the wide-hinged, spiriferoid-like triplesiaeid first recorded by M'Coy (1851: 402) as *Strophomena spiriferoides* and now known to belong to a well-distributed generic stock, *Bicuspina* Havlíček. Although European species range from Llandeilian to late Caradocian in age (Havlíček 1950: 88), it appears that the British species is much more restricted and it is generally supposed to be pre-eminently characteristic of the Longvillian stage although this belief still requires confirmation and in any case it is important to know what precisely is meant by "*Strophomena*" *spiriferoides*.

M'Coy's description is quite exhaustive and although no one can doubt that during its preparation he had the *Bicuspina* kind of shell in mind, it is not accompanied by any illustrations and is clearly a generalized statement covering a number of specimens (twenty-seven of them are still preserved in the Sedgwick Museum) that had been taken from at least eleven localities in North Wales and the Welsh borderlands. In attempting to restrict the species to specimens collected from certain rocks exposed in one locality, no precedence need be attached to his list of occurrences (M'Coy 1851: 402) which was obviously drawn up without any intention of order. The Bala district, however, was evidently his chief source of material because he records the stock from four distinct exposures, in the vicinity of that town, of what are now known to be ashes and limestones of the Gelli-grŷn Group. Moreover, when he issued an almost identical description of the species



(M'Coy 1852 : 246), the only noteworthy additions were two rather stylized drawings of the internal moulds of a brachial (left-hand figure) and a pedicle (right-hand figure) valve. While it is impossible to be certain in this matter, it seems very likely that the right-hand figure was based on a mould (A.42458) recorded as from the "Limestone schists of Bala"; the left-hand figure is probably a composite reconstruction for there is no reasonable model for it among the specimens used by M'Coy. On the strength, then, of this identification and the preponderance of specimens from the Bala district in the collection examined by M'Coy, it is reasonable to choose lectotypes known from lithology and record to have been recovered from the Gelli-grŷn Group. The exact locality is conjectural. In both descriptions M'Coy refers to specimens from "schists of Bryn Melyn" as well as those of "Gelli-Grŷn", "Tan y Bwlch y Groes" and "Garneidd Uchaf". Specimens from the last three outcrops are so identified in the collection, but none is attributed to the Bryn Melyn outcrop and since the lectotypes were chosen from the only lot labelled simply as "Limestone Schists Bala" it could well be that these actually were taken from the ashy limestones cropping out near Bryn Melyn.

There is not a great deal more to be said about the morphological variability of the species as thus restricted because, although moulds of both valves are common enough in the Gelli-grŷn Group, they are mostly too deformed to be used for more than generic identification and the proportions given in the diagnosis represent averages for between 2 and 5 specimens. The radial ornamentation, however, does require some comment. It consists of evenly rounded costellae with a wavelength of 0.3, 0.4 and 0.5 mm., 10 mm. antero-medially of the ventral umbones of 2, 2 and 4 specimens respectively. These consistent measurements are a reflection of the regularity with which new costellae arise either by intercalation or by branching from the 20 or so primary costae originating at the umbo. The complex pattern of ribs within the sulcus (a complementary arrangement is to be expected on the fold) has been traced from its origin in only two valves. In both, a median costa arising at the beak bifurcated to form a submedian pair and within 2 mm. another median rib had appeared, either by intercalation or by branching from the left submedian one, so that basically a triad of costae with ancillary branches and intercalations occupied the floor of the sulcus. In addition to these, internal branches from the primary costae occupying the shoulders of the sulcus "migrated", with the enlargement of the valve, down the sides ultimately to occupy the lateral segments of the floor. The first pair of these lateral branches can arise early but they are invariably later than the dichotomy of the original median primary and in 10 out of 12 valves they also appeared later than the second median costa.

Moulds of *Bicuspina* are also found in the highest Allt Ddu sandstones and mudstones and very rarely in siltstones just above the Frondderw Ash; at present they are indistinguishable from *B. spiriferoides* s.s. The Czechoslovakian species *B. cava* (Barrande) and *B. multicostellata* Havlíček, which have been identified in Llandeilo and Lower Caradoc rocks (see Havlíček 1950 : 88-89) differ greatly from the British species in the very much greater relative length of the valves, the weakness or even absence of the fold and sulcus and the fineness of the radial ornamentation.



Genus *OXOPLECIA* Wilson 1913

TYPE SPECIES. *Oxoplectia calhouni* Wilson by original designation of Wilson (1913 : 81).

*Oxoplectia* sp.

(Pl. 10, figs. 11-13, 17)

DESCRIPTION. Subcircular, biconvex *Oxoplectia* with a short hinge-line and obtuse cardinal angles, brachial valve over four-fifths as long as wide and over one-quarter as deep as long with a high rounded fold less than one-half as wide as the valve is long, sulcus in pedicle valve correspondingly deep with steep lateral slopes ; concentric lamellae on the shell-exterior, consistently developed and fine, numbering about 9 per mm., 5 mm. anterior of the ventral umbo ; radial ornamentation well developed within 2 mm. of the umbones and consisting of well-rounded costae attaining a wavelength of up to 0.7 mm. before dividing, in the sulcus up to 5 ribs appear in valves up to 8 mm. long but at least 2 of these can arise by branching or implantation ; on the fold 3 costae first developed but the median and right lateral ones branched dichotomously within a few millimetres of the dorsal umbo so that with further branching as many as 9 costae and costellae occur on the crest of the fold ; as many as 9 costae occur on each flank with the pair adjacent to the fold or sulcus giving rise to freely developed external and internal costellae ; dental lamellae short and divergent ; cardinal process bifurcating early, socket ridges ankylosed to the base of the cardinal process and subtriangular in outline, dorsal adductor muscle field quadripartite about the fold with the larger subtriangular anterior pair separated from the posterior by a pair of curved depressions.

## MATERIAL (Figured).

|                                                           | length | width (mm.) |
|-----------------------------------------------------------|--------|-------------|
| Incomplete external mould of<br>pedicle valve (BB.29035)  | 9.0    | —           |
| Incomplete internal mould of<br>pedicle valve (BB.24622)  | —      | —           |
| Incomplete external mould of<br>brachial valve (BB.29037) | 12.0   | —           |
| Incomplete internal mould of<br>brachial valve (BB.29038) | —      | —           |

HORIZON AND LOCALITIES. Gelli-grîn Group : all specimens from calcareous ash crags 75 ft. south of east end of ruined building in Ffridd Bach, south of Maes-meillion.

DISCUSSION. A few incomplete moulds of a species of *Oxoplectia* have been recovered from the Gelli-grîn Group and have been described because they differ importantly from the other species recorded from the Caradocian rocks of North Wales, namely *O. mutabilis* Williams (see Whittington & Williams 1955 : 411) from the Derfel limestone, especially in the relatively wider dorsal fold and in the development of radial ornamentation in early stages of growth. In respect of these features, the Bala moulds are like *Oxoplectia dorsata* (Hisinger) as redescribed by Öpik (1930 : 200) but are less quadrate in outline and until the significance of this difference can be assessed it seems appropriate not to assign a specific status to them.



Superfamily CLITAMBONITACEA Winchell & Schuchert 1893

Family CLITAMBONITIDAE Winchell & Schuchert 1893

Genus **VELLAMO** Öpik 1930

TYPE SPECIES. *Orthis verneuili* Eichwald by original designation of Öpik (1930 : 212).

***Vellamo*** sp.

(Pl. 10, figs. 14, 18)

The external and internal moulds (BB.28965, BB.29133) of a broken pedicle valve, collected from mudstones of the Allt Ddu Group on the moorland 1,950 ft. east of Llaithgwm Farm, are the only clitambonitaceid remains yet recorded in the Caradocian rocks of the Bala district. The valve which was about 9 mm. long and 5.5 mm. deep, was transversely subpentagonal in outline but asymmetrical due to impeded growth of the left half, and subpyramidal in profile with a slight median sulcus indenting the anterior commissure. The surface was ornamented by strong costae and costellae, rounded in profile and with a wave-length of about 0.5 mm. at the anterior margin. About 20 arose within 3 mm. of the umbo and thereafter branched evenly to be interrupted at irregular intervals by "growth lines". Judging from better preserved parts of the external mould, the shell surface was also ornamented by fine concentric lines with an incidence of 8 between 3 and 4 mm. anterior of the umbo, but these are never extravagantly developed as lamellae in the manner of *Clitambonites* and the valve is certainly best assigned to the genus *Vellamo*. The internal mould is incomplete and shows only the slot for a median ridge which must have extended anterior of the spondylium in the manner typical of the clitambonitids.

In both profile and outline as well as the median sulcus and the multicostellate radial ornamentation, the valve is clearly related to the *V. pyramidalis* (Pahlen) species group (see Öpik 1930 : 213-217) but more material will have to be obtained before specific identification is attempted.

Superfamily PLECTAMBONITACEA Kozłowski 1929

Family LEPTELLINIDAE Ulrich & Cooper 1936

Genus **LEPTESTIINA** Havlíček 1952

TYPE SPECIES. *Leptestiina prantli* Havlíček by original designation of Havlíček (1952 : 13).

***Leptestiina oepiki*** (Whittington)

(Pl. 10, figs. 15, 16, 19-21)

1938 *Sampo oepiki* Whittington : 255, pl. 10, figs. 15-16, pl. 11, fig. 10.

DIAGNOSIS (emended). Semi-circular and evenly concavo-convex *Leptestiina* with pedicle valve almost three-fifths as long as wide and over two-fifths as deep as long ; radial ornamentation unequally parvicostellate with fine costellae, about



7 or 8 per mm., segregated into sectors up to 1.5 mm. wide by conspicuous, thickened ribs three of which, a lateral pair subtending an angle of about  $90^\circ$  and symmetrical about a median one, arise at the umbo, additional thickened costellae arise beyond the 1 mm. growth stage maintaining the regularity of the sectors so that in valves 5 mm. long, about nine of varying length occur; concentrically arranged, interrupted comae incipiently developed especially on ventral surface; ventral interarea apsacline, pseudodeltidium small and apical, foramen closed; dorsal interarea hypercline, chilidial plates well developed; teeth and accessory nodes buttressed by short receding dental lamellae, ventral muscle field transversely subpentagonal in outline, extending anteriorly for less than one-third the length of pedicle valve and about three-quarters as long as wide, adductor field lanceolate, commonly divided medianly by low ridge and deeply inserted, especially posteriorly, into thick shell substance of umbonal cavity, diductor scars almost meeting anteriorly to enclose adductor scar and divided into pair of narrow, submedian lobes encroaching on *vascula media* and broad pair of lateral lobes, ventral pallial sinus pattern lemniscate; cardinal process consisting of simple, median ridge supported by thickened notothyrial platform passing anteriorly into low, broad median ridge which bifurcates about the deep incision of the lophophore platform, socket ridges widely disposed, subparallel with hinge-line to define a pair of oval sockets; lophophore platform about three-fifths as long as brachial valve, and about three-quarters as long as wide, defined posteriorly as pair of widely divergent ridges confluent with bases of socket ridges but strongly undercut and medianly incised anteriorly and ornamented by about 20 radiating ridges; adductor scars vaguely impressed on either side of median ridge; dorsal pallial sinus pattern lemniscate.

MATERIAL (Figured).

|                                                     | length | width (mm.) |
|-----------------------------------------------------|--------|-------------|
| Deformed internal mould of pedicle valve (BB.28886) | 7.0    | 9.5         |
| Internal mould of pedicle valve (BB.28890)          | 6.0    | 9.0         |
| External mould of brachial valve (BB.28889)         | 5.0    | 10.0        |
| External mould of pedicle valve (BB.28888)          | 5.5    | —           |
| Internal mould of brachial valve (BB.28891)         | 5.5    | —           |

HORIZON AND LOCALITIES. Gelli-grŷn Group: BB.28886 from calcareous ashes exposed on the north side of the central outlier of Rhiwlas Limestone on Creigiau Bychain; BB.28888-91 from calcareous ashes above the limestone in the old quarries in Ffridd Bach, south of Maes-meillion.

DISCUSSION. This species occurs rarely in the Longvillian of Wales and the Welsh Borderlands and has been redescribed because the moulds obtained from the Gelli-grŷn Group were adequate in both preservation and numbers to show that



the stock is more appropriately assigned to *Leptestiina* and to provide some comparative evaluation of its general morphology. The pedicle valves were almost semi-circular in outline and strongly and evenly convex with a mean percentage length relative to width (with variance) of 57.8 (66.43) for 8 moulds and a mean percentage depth relative to length of 44 (range 38–52) for 3 moulds. The ornamentation is usually poorly preserved but the sporadic occurrence of comae with the suggestions of a concentric disposition and especially the segregation of the fine costellae into sectors by the excessive thickening of regularly spaced costae and costellae are noteworthy. The ventral muscle field is unexceptional in arrangement: in 5 internal moulds the mean percentage length relative to that of the valve was 31.0 (variance 24.0) and its transversely subpentagonal outline is reflected in a mean percentage length relative to width of 75.4 (variance 154.67) in 9 moulds. The interior of the brachial valve was dominated by the deeply incised subrectangular lophophore platform with semi-circular undercut anterior margins. In 3 dorsal internal moulds the mean percentage length of the lophophore platform relative to that of the valve was 60.7 (range 56–64) and in 9 moulds the mean percentage length of the platform relative to width (with variance) was 76.2 (59.75).

The species is closely related to *Leptestiina derfelensis* (Jones 1928 : 479–481 ; see also Whittington & Williams 1955 : 415) and in the absence of good samples it is difficult to assess the importance of those differences which appear to distinguish the two stocks. Certainly in shell outline, both are comparable and although *L. oepiki* is possibly more deeply convex and bears umbonally 3 thickened costae in contrast to 5 reported for *L. derfelensis*, better preserved material may show that the differences are not really significant. Internally, the ventral muscle field may prove to be longer relative to the length of the valve but the most important distinction is probably in the different shapes of the lophophore platform which is less than three-fifths as long as wide in *L. derfelensis*.

### Family SOWERBYELLIDAE Öpik 1930

#### Genus **SOWERBYELLA** Jones 1928

TYPE SPECIES. *Leptaena sericea* J. de C. Sowerby by original designation of Jones (1928 : 384).

#### ***Sowerbyella sericea*** (J. de C. Sowerby)

(Pl. 11, figs. 1–9 ; Text-figs. 11, 12)

1839 *Leptaena sericea* J. de C. Sowerby: 636, pl. 19, fig. 1.

1928 *Sowerbyella sericea* (J. de C. Sowerby) Jones : 414, pl. 21, figs. 1–4.

DIAGNOSIS (emended). Semi-circular *Sowerbyella* with evenly concavo-convex longitudinal profile rarely modified by low narrow median fold in pedicle valve, cardinal angles acute in young stages of growth but commonly becoming rectangular or even obtuse in adult shells, pedicle valve less than two-thirds as long as wide and



over one-quarter as deep as long ; radial ornamentation unequally parvicostellate commonly with 7 or 8 costellae per mm., 10 mm. antero-medially of dorsal umbo, segregated into sectors about 0.8 mm. wide, postero-lateral areas also commonly ornamented by rugae with wavelength of 0.3 mm. disposed acutely to hinge-line and commonly forming 4 pairs extending antero-medially through sectors of up to 25°, pseudodeltidium and chilidium small, apical ; teeth small, dental lamellae obsolescent in adult shells ; ventral muscle field deeply cordate in outline over three-quarters as long as wide and extending anteriorly for just over one-half the length of pedicle valve, adductor scars small, lanceolate, inserted posteriorly into callist beneath pseudodeltidium, and divided by median septum extending anteriorly for about one-quarter the length of valve, diductor scars widely separated anteriorly and split by divergent *vascula media* ; ventral pallial sinus pattern lemniscate ; cardinalia about one-third as long as wide, extending anteriorly for about one-eighth the length of brachial valve and consisting of median cardinal process fused with chilidial plates and widely divergent socket ridges, notothyrial platform not conspicuously hollowed, submedian septa narrowly divergent, extending anteriorly for nearly three-quarters the length of valve, "lophophore" platform elevated, divided by *vascula myaria* and nearly one-fifth as wide again as length of submedian septa that form its inner boundaries ; low median ridge commonly developed between submedian septa in brachial valves over 5 mm. long ; pallial sinus pattern lemniscate.



FIG. 11. The dorsal (a) and ventral (b) internal moulds of *Sowerbyella sericea* (J. de C. Sowerby),  $\times 3$  approx., showing the pallial sinus patterns : gg, *vascula genitalia* ; m, *vascula media* ; y, *vascula myaria*.

#### MATERIAL (Figured).

|                                               | length | width (mm.) |
|-----------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.29064) | 8.5    | 14.0        |
| Internal mould of pedicle valve<br>(BB.29065) | 11.0   | 19.5        |
| Internal mould of pedicle valve<br>(BB.29066) | 5.0    | 9.5         |



| MATERIAL (Figured) ( <i>continued</i> ).       | length | width (mm.) |
|------------------------------------------------|--------|-------------|
| Internal mould of brachial valve<br>(BB.29067) | 8.0    | 14.5        |
| Internal mould of brachial valve<br>(BB.29068) | 3.6    | 6.2         |
| Internal mould of brachial valve<br>(BB.29069) | —      | 21.0        |
| External mould of brachial valve<br>(BB.29070) | 3.5    | 6.0         |
| External mould of brachial valve<br>(BB.29071) | 8.0    | 14.0        |
| External mould of pedicle valve<br>(BB.29072)  | 10.0   | 17.0        |

HORIZON AND LOCALITY. Upper Longvillian Substage : all specimens from the Alternata Limestone exposed at Soudley Quarry, 2 miles south-east of Church Stretton, Shropshire.

### *Sowerbyella soudleyensis* Jones

(Pl. 12, figs. 1-8)

1928 *Sowerbyella sericea* (J. de C. Sowerby) var. *soudleyensis* Jones : 417, pl. 21, figs. 5, 6.

DIAGNOSIS. Semi-circular *Sowerbyella* with concavo-convex profile commonly modified by narrow median fold in pedicle valve, cardinal angles acute to rectangular in adult shells, pedicle valve just over one-half as long as wide and about one-third as deep as long ; radial ornamentation unequally parvicostellate commonly with 8 costellae per mm., 10 mm. antero-medially of dorsal umbo, segregated in sectors about 1 mm. wide, postero-lateral areas also commonly ornamented by rugae with wavelength of 0.3 mm., disposed acutely to hinge-line and commonly forming 3 pairs extending antero-medially through sectors of up to 25°, pseudodeltidium and chilidium small, apical ; teeth small, dental lamellae obsolescent in adult shells, ventral muscle field deeply cordate in outline about three-quarters as long as wide and extending anteriorly for just over one-half the length of pedicle valve, adductor scars small, lanceolate, inserted posteriorly into callist beneath pseudodeltidium and divided by median septum extending anteriorly for about one-quarter the length of valve, diductor scars widely separated anteriorly and split by divergent *vascula media* contributing to a lemniscate pallial sinus pattern ; cardinalia about one-third as long as wide, extending anteriorly for about one-eighth the length of brachial valve and consisting of median cardinal process fused with chilidial plates and widely divergent socket ridges, notothyrial platform commonly not conspicuously hollowed ; submedian septa narrowly divergent, extending anteriorly for about seven-tenths the length of valve, "lophophore" platform elevated and



tending to be undercut along its anterior margin and nearly one-third as wide again as the length of submedian septa that form its inner boundary ; low median ridge commonly developed between submedian septa in brachial valves over 5 mm. long ; pallial sinus pattern lemniscate.

| MATERIAL (Figured).                                             | length | width (mm.) |
|-----------------------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.29073)                   | 8.0    | 12.5        |
| Exfoliated exterior of pedicle valve<br>(BB.29074)              | 7.2    | —           |
| Internal mould of pedicle valve<br>(BB.29075)                   | 5.5    | 11.5        |
| External and internal moulds of<br>pedicle valve (BB.29076-77)  | 3.2    | 6.0         |
| External and internal moulds of<br>brachial valve (BB.29078-79) | 2.8    | —           |
| Internal mould of brachial valve<br>(BB.29080)                  | 5.0    | 9.5         |
| External mould of brachial valve<br>(BB.29081)                  | 7.0    | 14.0        |
| External mould of brachial valve<br>(BB.29082)                  | 5.8    | 10.0        |

HORIZON AND LOCALITY. Lower Longvillian Substage : all specimens topotypic with those used by Jones (1928 : 417-418) to establish the variety *S. sericea* var. *soudleyensis* and obtained from green-weathering sandstones exposed in an old quarry on the roadside south of Whittingslow, Shropshire.

***Sowerbyella musculosa* sp. nov.**

(Pl. II, figs. 18-27)

DIAGNOSIS. Semi-circular *Sowerbyella* with pedicle valve just over one-half as long as wide and nearly two-fifths as deep as long with evenly concavo-convex longitudinal profile, rarely subcarinate or obscurely uniplicate, cardinal angles rarely rectangular or obtuse in adult shells ; radial ornamentation unequally parvicostellate commonly with 9 costellae per mm., 10 mm. antero-medially of dorsal umbo, and commonly segregated into sectors about 0.7 mm. wide ; postero-lateral areas also commonly ornamented by 3 pairs of short rugae with wavelength of about 0.3 mm. and disposed acutely to hinge-line ; ventral muscle field deeply cordate in outline, nearly as long as wide and extending anteriorly for less than one-half the length of pedicle valve, median septum separating small lanceolate adductor scars, extending anteriorly for about one-quarter the length of valve and merging posteriorly with callist ; cardinalia over two-fifths as long as wide and extending anteriorly for less than one-fifth the length of brachial valve, notothyrial



platform tending to be hollowed, submedian septa narrowly divergent, extending anteriorly for about two-thirds the length of valve commonly containing median ridge in valves over 2.5 mm. long, "lophophore" platform strongly elevated, over one-third as wide again as the length of submedian septa.

|            |                                                              | length | width (mm.) |
|------------|--------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | External and internal moulds of pedicle valve (BB.29083-84)  | 4.2    | 7.5         |
| PARATYPES. | External and internal moulds of pedicle valve (BB.29085-86)  | 3.0    | 5.3         |
|            | External and internal moulds of brachial valve (BB.29087-88) | 2.8    | 6.0         |
|            | Internal mould of brachial valve (BB.29089)                  | 5.5    | 10.0        |
|            | External mould of pedicle valve (BB.29090)                   | 3.2    | 7.0         |
|            | Incomplete internal mould of pedicle valve (BB.28895)        | 6.5    | —           |
|            | External mould of pedicle valve (BB.29091)                   | 4.5    | 8.0         |
|            | External mould of pedicle valve (BB.29092)                   | 5.5    | —           |

HORIZON AND LOCALITY. Allt Ddu Group : all specimens from fine sandstones and mudstones immediately below the Pont-y-Ceunant Ash and exposed in crags north of the drive to Y Garnedd Farm.

*Sowerbyella sericea* (J. de C. Sowerby) ***permixta*** subsp. nov.  
(Pl. II, figs. 10-17)

DIAGNOSIS. Semi-circular *Sowerbyella* with pedicle valve over one-half as long as wide and about one-third as deep as long with evenly concavo-convex longitudinal profile, rarely subcarinate or shallowly uniplicate ; cardinal angles rarely rectangular or obtuse in adult shells ; radial ornamentation unequally parvicostellate commonly with 9 costellae per mm., 10 mm. antero-medianly of dorsal umbo, and segregated into sectors about 0.6 mm. wide ; postero-lateral areas also commonly ornamented by 4 pairs of short rugae, with wavelength of about 0.3 mm. and disposed acutely to hinge-line ; ventral muscle field deeply cordate in outline nearly four-fifths as long as wide and extending anteriorly for about one-half the length of pedicle valve, median septum separating small, lanceolate adductor scars, extending anteriorly for nearly one-quarter the length of valve and merging posteriorly with callist ; cardinalia nearly two-fifths as long as wide and extending anteriorly for about



one-eighth the length of brachial valve, notothyrial platform not greatly hollowed, submedian septa narrowly divergent, extending anteriorly for about two-thirds the length of valve commonly containing a median ridge in valves over 2.5 mm. long, "lophophore" platform elevated, less than one-fifth as wide again as the length of submedian septa.

|            |                                                | length | width (mm.) |
|------------|------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal mould of brachial valve<br>(BB.29093) | 6.5    | 12.0        |
| PARATYPES. | Internal mould of brachial valve<br>(BB.29094) | 3.0    | —           |
|            | Internal mould of brachial valve<br>(BB.29095) | 1.8    | 3.7         |
|            | Internal mould of brachial valve<br>(BB.29096) | 4.0    | 8.0         |
|            | External mould of brachial valve<br>(BB.29097) | 5.0    | 10.5        |
|            | External mould of brachial valve<br>(BB.29098) | 5.0    | 9.0         |
|            | Internal mould of pedicle valve<br>(BB.29099)  | 6.5    | —           |
|            | Internal mould of pedicle valve<br>(BB.29100)  | 8.0    | 13.5        |

HORIZON AND LOCALITIES. BB.29093-99 from mudstones of the Nant Hir Group exposed in left bank of Nant Hir, 600 ft. north-east of Cefn-y-maes Farm; BB.29100 from fine sandstones of the Glyn Gower Group exposed as crags in field, 1,100 ft. west of Y Fedw Farm.

DISCUSSION. The genus *Sowerbyella* is well represented at most fossiliferous horizons within the Caradocian successions of the Bala district and three samples, comprising associates of *Dinorthis berwynensis angusta* subsp. nov. and *Heterorthis retrorsistria* (M'Coy) from the upper and lower parts respectively of the Allt Ddu Group as well as a composite lot from the Upper Glyn Gower and Nant Hir Groups have been used to assess any changes that might have taken place. The youngest forms were probably contemporaries of *S. soudleyensis* (Jones) that abounds in the Lower Longvillian rocks of the Welsh Borders. This latter species was originally described by Jones (1928 : 417) as a variety of *S. sericea* (J. de C. Sowerby) but a study of two good collections of topotypic material shows that these two stocks are unlike in a number of features and are better treated as two distinct species in the manner described above. Further, when these are compared with the Bala specimens, it becomes evident that the bulk of the Welsh shells are only slightly different from *S. sericea* whereas those from the top of the Allt Ddu Group are quite distinct from all known stocks and so a new subspecies, *S. sericea permixta*, and a new species, *S. musculosa*, have been proposed in recognition of these differences.



TABLE 82

|                           | A | B         | C         | D         | E        |
|---------------------------|---|-----------|-----------|-----------|----------|
| l mm                      | . | 5.39      | 3.15      | 7.1       | 4.69     |
| (var. l) .                | . | (1.997)   | (1.093)   | (3.504)   | (5.668)  |
| w mm.                     | . | 10.07     | 6.29      | 12.55     | 8.78     |
| (var. w) .                | . | (5.253)   | (3.49)    | (9.658)   | (16.478) |
| r .                       | . | 0.927     | 0.969     | 9.971     | 0.984    |
| log <sub>e</sub> l        | . | 1.651     | 1.0952    | 1.9262    | 1.4306   |
| (var. log <sub>e</sub> l) | . | (0.0669)  | (0.1044)  | (0.0677)  | (0.2295) |
| log <sub>e</sub> w        | . | 2.2841    | 1.7967    | 2.4996    | 2.0760   |
| (var. log <sub>e</sub> w) | . | (0.0507)  | (0.0846)  | (0.0602)  | (0.1930) |
| r <sub>e</sub> .          | . | 0.979     | 0.978     | 0.959     | 0.964    |
| α .                       | . | 0.989     | 0.9002    | 0.943     | 0.9171   |
| (var. α) .                | . | (0.00099) | (0.00121) | (0.00476) | (0.0033) |

TABLE 82. Statistics of length (l) and maximum width (w) of 43 pedicle valves of *Sowerbyella sericea* (J. de C. Sowerby) (A), 36 of *S. souldleyensis* Jones (B), 31 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 17 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 20 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 83

|                            | A               | B               | C               | D               | E               |
|----------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| l mm.                      |                 |                 |                 |                 |                 |
| (var. l)                   | 7.06<br>(3.752) | 5.15<br>(1.48)  | 3.6<br>(1.808)  | 6.63<br>(5.836) | 4.94<br>(5.515) |
| th mm.                     |                 |                 |                 |                 |                 |
| (var. th)                  | 2.01<br>(0.662) | 1.79<br>(0.333) | 1.39<br>(0.415) | 2.45<br>(1.178) | 1.58<br>(0.836) |
| r                          | 0.819           | 0.895           | 0.884           | 0.957           | 0.971           |
| log <sub>e</sub> l         | 1.9181          | 1.6117          | 1.2154          | 1.8296          | 1.4955          |
| (var. log <sub>e</sub> l)  | (0.0725)        | (0.0545)        | (0.1310)        | (0.1239)        | (0.2037)        |
| log <sub>e</sub> th        | 0.6239          | 0.5328          | 0.232           | 0.8065          | 0.3129          |
| (var. log <sub>e</sub> th) | (0.1484)        | (0.0988)        | (0.1946)        | (0.1792)        | (0.2889)        |
| r <sub>e</sub>             | 0.807           | 0.898           | 0.91            | 0.95            | 0.985           |
| α                          | 1.43            | 1.346           | 1.219           | 1.202           | 1.19            |
| (var. α)                   | (0.01587)       | (0.01098)       | (0.008)         | (0.01282)       | (0.00302)       |

TABLE 83. Statistics of length (l) and maximum depth (th) of 47 pedicle valves of *Sowerbyella sericea* (J. de C. Sowerby) (A), 34 of *S. souldleyensis* Jones (B), 34 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 13 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 16 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 84

|            | A         | B         | C         | D         | E         |
|------------|-----------|-----------|-----------|-----------|-----------|
| l mm.      | .         | 5.36      | 3.2       | 7.29      | 5.95      |
| (var. l) . | (3.875)   | (1.756)   | (1.699)   | (3.929)   | (2.563)   |
| s mm.      | 1.72      | 1.41      | 0.82      | 1.66      | 1.33      |
| (var. s) . | (0.219)   | (0.15)    | (0.158)   | (0.218)   | (0.131)   |
| r .        | 0.946     | 0.848     | 0.84      | 0.91      | 0.863     |
| a .        | 0.2377    | 0.2922    | 0.305     | 0.2356    | 0.2261    |
| (var. a) . | (0.00011) | (0.00051) | (0.00082) | (0.00033) | (0.00041) |

TABLE 84. Statistics of length of pedicle valve (l) and length of septum within the ventral muscle field (s) for 59 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 50 of *S. souldleyensis* Jones (B), 35 of *S. musculosa* sp. nov. from the top of the Alt Ddu Group (C), 31 of *S. sericea permixta* subsp. nov. from the Lower Alt Ddu Group (D) and 34 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 85

|                           | A        | B         | C         | D         | E         |
|---------------------------|----------|-----------|-----------|-----------|-----------|
| $\bar{l}$ mm.             | 7.06     | 5.48      | 3.61      | 7.4       | 6.41      |
| (var. $\bar{l}$ )         | (3.964)  | (1.916)   | (2.397)   | (3.524)   | (1.676)   |
| $\bar{sc}$ mm.            | 3.68     | 2.98      | 1.69      | 3.84      | 3.21      |
| (var. $\bar{sc}$ )        | (1.581)  | (0.825)   | (0.716)   | (1.313)   | (0.587)   |
| $r$                       | 0.947    | 0.963     | 0.781     | 0.959     | 0.919     |
| $\log_e \bar{l}$          | 1.9159   | 1.67      | 1.1992    | 1.9699    | 1.8378    |
| (var. $\log_e \bar{l}$ )  | (0.077)  | (0.0621)  | (0.169)   | (0.0631)  | (0.0402)  |
| $\log_e \bar{sc}$         | 1.2476   | 1.0473    | 0.4131    | 1.3027    | 1.1385    |
| (var. $\log_e \bar{sc}$ ) | (0.1105) | (0.0891)  | (0.2231)  | (0.0856)  | (0.0555)  |
| $r_e$                     | 0.934    | 0.961     | 0.8       | 0.947     | 0.91      |
| $\alpha$                  | 1.198    | 1.198     | 1.149     | 1.165     | 1.175     |
| (var. $\alpha$ )          | (0.003)  | (0.00239) | (0.02374) | (0.00467) | (0.00719) |

TABLE 85. Statistics of length of pedicle valve ( $\bar{l}$ ) and length of ventral muscle scar ( $\bar{sc}$ ) for 63 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 48 of *S. soudleyensis* Jones (B), 22 of *S. musculosa* sp. nov. from the top of the Alt Ddu Group (C), 32 of *S. sericea permixta* subsp. nov. from the Lower Alt Ddu Group (D) and 35 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 86

|                           | A | B         | C         | D         | E         |
|---------------------------|---|-----------|-----------|-----------|-----------|
| l mm.                     |   | 3.12      | 1.79      | 3.78      | 3.17      |
| (var. l)                  | . | (0.684)   | (0.757)   | (0.803)   | (0.845)   |
| w mm.                     | . | 4.08      | 1.83      | 4.63      | 4.06      |
| (var. w)                  | . | (1.093)   | (0.522)   | (1.123)   | (1.38)    |
| r                         | . | 0.905     | 0.936     | 0.976     | 0.949     |
| log <sub>e</sub> l        | . | 1.1039    | 0.4763    | 1.3024    | 1.1133    |
| (var. log <sub>e</sub> l) | . | (0.0677)  | (0.2118)  | (0.054)   | (0.0808)  |
| log <sub>e</sub> w        | . | 1.3741    | 0.5318    | 1.5972    | 1.3608    |
| (var. log <sub>e</sub> w) | . | (0.064)   | (0.145)   | (0.0507)  | (0.0808)  |
| r <sub>e</sub>            | . | 0.93      | 0.945     | 0.988     | 0.953     |
| α                         | . | 0.9723    | 0.8274    | 0.969     | 1.0       |
| (var. α)                  | . | (0.00376) | (0.00431) | (0.00173) | (0.00655) |

TABLE 86. Statistics of length (l) and maximum width (w) of the ventral muscle scar in 57 pedicle valves of *Sowerbyella sericea* (J. de C. Sowerby) (A), 36 of *S. soudleyensis* Jones (B), 19 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 15 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 16 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 87

|                    | A         | B         | C         | D        | E         |
|--------------------|-----------|-----------|-----------|----------|-----------|
| l mm.              |           | 5.42      | 3.05      | 5.94     | 5.29      |
| (var. l)           | 6.19      | (3.196)   | (1.571)   | (4.503)  | (4.322)   |
| s mm.              | (4.562)   | 3.89      | 2.10      | 4.07     | 3.48      |
| (var. s)           | 4.51      | (1.94)    | (0.699)   | (2.202)  | (2.169)   |
| r                  | (2.77)    | 0.974     | 0.967     | 0.974    | 0.968     |
| log <sub>e</sub> l | 0.96      | 1.6385    | 1.037     | 1.722    | 1.5941    |
| (var. loge l)      | 1.7668    | (0.1031)  | (0.1562)  | (0.1194) | (0.1433)  |
| log <sub>e</sub> s | (0.1122)  | 1.2982    | 0.6685    | 1.3412   | 1.1646    |
| (var. loge s)      | 1.4426    | (0.1203)  | (0.1468)  | (0.1248) | (0.1648)  |
| r <sub>e</sub>     | (0.1274)  | 0.981     | 0.975     | 0.971    | 0.96      |
| α                  | 0.959     | 1.08      | 0.964     | 1.022    | 1.072     |
| (var. α)           | 1.065     | (0.00112) | (0.00101) | (0.0026) | (0.00117) |
|                    | (0.00175) |           |           |          |           |

TABLE 87. Statistics of the length of the brachial valve (l) and the length of the submedian septas from the dorsal umbo of 59 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 41 of *S. souldleyensis* Jones (B), 48 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 25 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 79 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 88

|                           | A         | B        | C         | D         | E         |
|---------------------------|-----------|----------|-----------|-----------|-----------|
| l mm.                     | 5.12      | 4.19     | 2.73      | 4.18      | 4.45      |
| (var. l) .                | (1.713)   | (1.317)  | (0.526)   | (1.126)   | (1.36)    |
| w mm.                     | 6.05      | 5.56     | 3.71      | 5.34      | 5.87      |
| (var. w) .                | (2.485)   | (2.698)  | (1.376)   | (2.055)   | (2.862)   |
| r .                       | 0.938     | 0.934    | 0.914     | 0.927     | 0.942     |
| log <sub>e</sub> l        | 1.6012    | 1.3964   | 0.9699    | 1.3987    | 1.4594    |
| (var. log <sub>e</sub> l) | (0.064)   | (0.0725) | (0.0687)  | (0.0631)  | (0.0669)  |
| log <sub>e</sub> w        | 1.7671    | 1.6737   | 1.2633    | 1.6404    | 1.7299    |
| (var. log <sub>e</sub> w) | (0.0659)  | (0.0837) | (0.0953)  | (0.0696)  | (0.0799)  |
| r <sub>e</sub> .          | 0.956     | 0.931    | 0.943     | 0.923     | 0.94      |
| α .                       | 1.015     | 1.074    | 1.178     | 1.05      | 1.093     |
| (var. α) .                | (0.00286) | (0.0053) | (0.00698) | (0.02334) | (0.00496) |

TABLE 88. Statistics of the length of the submedian septa from the dorsal umbo (l) and the width of the "lophophore platform" (w) of 33 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 31 of *S. souldleyensis* Jones (B), 24 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 9 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D), 30 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (E) and 30 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (F).



TABLE 89

|                           | A | B         | C         | D         | E         |
|---------------------------|---|-----------|-----------|-----------|-----------|
| l mm.                     |   | 5.07      | 3.14      | 6.29      | 5.21      |
| (var. l)                  | . | (2.698)   | (1.581)   | (2.928)   | (3.043)   |
| c mm.                     | . | 0.62      | 0.54      | 0.81      | 0.68      |
| (var. c)                  | . | (0.053)   | (0.052)   | (0.088)   | (0.07)    |
| r                         | . | 0.977     | 0.671     | 0.917     | 0.941     |
| log <sub>e</sub> l        | . | 1.5734    | 1.07      | 1.8032    | 1.5975    |
| (var. log <sub>e</sub> l) | . | (0.0997)  | (0.1484)  | (0.0715)  | (0.1061)  |
| log <sub>e</sub> c        | . | -0.5426   | -0.6982   | -0.2736   | -0.4561   |
| (var. log <sub>e</sub> c) | . | (0.1292)  | (0.164)   | (0.1257)  | (0.1407)  |
| r <sub>e</sub>            | . | 0.966     | 0.686     | 0.929     | 0.935     |
| α                         | . | 1.139     | 1.051     | 1.326     | 1.152     |
| (var. α)                  | . | (0.00321) | (0.01541) | (0.02007) | (0.00371) |

TABLE 89. Statistics of the length of the brachial valve (l) and the anterior extension of the socket ridges or brachiophores from the dorsal umbo (c) in 40 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 29 of *S. souldleyensis* Jones (B), 40 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 14 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 47 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



TABLE 90

|                    | A | B         | C         | D         | E         |
|--------------------|---|-----------|-----------|-----------|-----------|
| $\bar{l}$ mm.      |   | 0.63      | 0.56      | 0.76      | 0.73      |
| (var. l) .         | . | (0.0475)  | (0.049)   | (0.067)   | (0.082)   |
| $\bar{w}$ mm.      | . | 1.94      | 1.33      | 2.21      | 1.91      |
| (var. w) .         | . | (0.567)   | (0.351)   | (0.597)   | (0.644)   |
| $\bar{r}$ .        | . | 0.951     | 0.915     | 0.911     | 0.936     |
| $\log_e \bar{l}$   | . | -0.5187   | -0.6523   | -0.3292   | -0.3864   |
| (var. loge l)      | . | (0.1133)  | (0.145)   | (0.1096)  | (0.1433)  |
| $\log_e \bar{w}$   | . | 0.5923    | 0.1943    | 0.735     | 0.566     |
| (var. loge w)      | . | (0.1407)  | (0.1818)  | (0.1159)  | (0.1622)  |
| $\bar{r}_e$ .      | . | 0.968     | 0.9458    | 0.908     | 0.94      |
| $\alpha$ .         | . | 1.115     | 1.12      | 1.028     | 1.064     |
| (var. $\alpha$ ) . | . | (0.00155) | (0.00412) | (0.02318) | (0.00425) |

TABLE 90. Statistics of the anterior (l) and lateral (w) extension of the socket ridges or brachiophores from the dorsal umbo in 34 specimens of *Sowerbyella sericea* (J. de C. Sowerby) (A), 21 of *S. souldleyensis* Jones (B), 39 of *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), 10 of *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and 33 of *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



One of the most interesting aspects of the variability within the samples is the evidence presented in Table 92, that all Welsh stocks are more finely costellate than the Shropshire ones: and when exact probability tests are conducted for frequencies in cells of 6-8 and 9 or more costellae per mm., the differences are significant ( $p < 0.01$ ). It is tempting to correlate this difference with the finer sediments entombing the Bala shells but this remains to be demonstrated in other *Sowerbyella*. Certainly, phenotypic variation does not seem to have affected the development of rugae (Table 91) because although 4 pairs are most commonly developed in the new subspecies compared with 3 pairs in the other forms, the modes are not pronounced and there is almost complete overlap between all samples. Moreover the wavelengths are similar, ranging from 0.2 to 0.5 mm. but with modal estimates of 0.3 mm. in all 5 samples. In a like manner the change in the cardinal angles due to a decrease in the lateral expansion of the hinge-lines in later growth stages followed the same pattern. Thus taking *S. sericea* as an example the cardinal angles of shells less than 5 mm. long were mostly acute; but in longer shells the frequencies for acute, rectangular and obtuse angles were 7, 10 and 2.

TABLE 91

|   |   | 0 | 1 | 2  | 3  | 4  | 5 | 6 | 7 | 8 |
|---|---|---|---|----|----|----|---|---|---|---|
| A | . | 9 | — | 6  | 12 | 17 | 1 | 3 | 1 | — |
| B | . | 2 | — | 2  | 5  | 2  | — | — | — | 1 |
| C | . | 9 | 2 | 13 | 15 | 11 | 5 | 1 | — | — |
| D | . | 1 | 1 | —  | 5  | 6  | 1 | 1 | — | 1 |
| E | . | 3 | 2 | 2  | 5  | 7  | 6 | 1 | — | — |

TABLE 91. The frequencies of pedicle valves bearing the number of pairs of rugae given in the top row for *Sowerbyella sericea* (J. de C. Sowerby) (A), *S. soudleyensis* Jones (B), *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), *S. sericea permixta* subsp. nov. from the Lower Allt Ddu Group (D) and *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).

TABLE 92

|   |   | 6 | 7  | 8  | 9  | 10 | 11 | 12 |
|---|---|---|----|----|----|----|----|----|
| A | . | 3 | 24 | 20 | 6  | —  | —  | —  |
| B | . | — | 4  | 10 | 4  | —  | —  | —  |
| C | . | — | —  | —  | 2  | 6  | 4  | 2  |
| D | . | — | 3  | 10 | 10 | 5  | 2  | —  |
| E | . | — | 3  | 12 | 15 | 9  | 5  | 1  |

TABLE 92. The frequencies of brachial valves bearing the counts of costellae per mm. identified in the top row at a distance of 10 mm. antero-medially of the dorsal umbo for *Sowerbyella sericea* (J. de C. Sowerby) (A), *S. soudleyensis* Jones (B), *S. musculosa* sp. nov. from the top of the Allt Ddu Group (C), *S. sericea permixta* from the Lower Allt Ddu Group (D) and *S. sericea permixta* subsp. nov. from the Glyn Gower and Nant Hir Groups (E).



There was also a tendency for the pedicle valves to develop a narrow, rounded to sharp-crested, median fold (subcarina) or, very rarely, a slight median depression (uniplica). The number of pedicle valves, over 5 mm. long, with a subcarinate, unmodified or uniplicate profile respectively is as follows :

13, 40 and 0 for *S. sericea*

34, 12 and 0 for *S. soudleyensis*

2, 7 and 2 for *S. musculosa*

14, 18 and 0 for *S. sericea permixta* from the Lower Allt Ddu

and 7, 26 and 2 for *S. sericea permixta* from the Upper Glyn Gower and Nant Hir Groups. *S. soudleyensis* is clearly distinct from all other samples in the commonness of the subcarinate condition.

|                            |                                                                                                                    |                                                                                   |                                                                     |
|----------------------------|--------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------|---------------------------------------------------------------------|
| <i>S. soudleyensis</i>     | <div> <math>b_2</math> <math>a_1</math> </div> <div>k</div> <div> <math>c_1</math> </div>                          |                                                                                   |                                                                     |
| <i>S. musculosa</i>        | <div> <math>e_1 f_2 h_1</math> <math>a_1</math> </div> <div>l</div> <div> <math>g_1</math> <math>c_1</math> </div> | <div> <math>e_2 f_2 h_1</math> </div> <div>kl</div> <div> <math>g_2</math> </div> |                                                                     |
| <i>S. sericea permixta</i> | <div> <math>g_2</math> </div> <div>l</div>                                                                         | <div> <math>g_2</math> </div> <div>kl</div> <div> <math>c_1</math> </div>         | <div> <math>e_2 f_2 h_1</math> </div> <div> <math>c_1</math> </div> |
|                            | <i>S. sericea</i>                                                                                                  | <i>S. soudleyensis</i>                                                            | <i>S. musculosa</i>                                                 |

FIG. 12. The distribution of significant differences between any two named species of *Sowerbyella* where a and b respectively represent the relative width and depth of the pedicle valve, c the relative length of the ventral septum, e the relative width of the ventral muscle scar, f and g respectively the relative length and width of the cardinalia, h the relative length of the dorsal submedian septa, i the ventral median fold and l the incidence of costellae per mm.: lower case figures 1 or 2 respectively indicate significant differences in growth rate or inherent shape.



Nine bivariate estimates of relative growth have been calculated for all five samples. They are indices of the outline and profile of the pedicle valve, the outline and relative length of the ventral muscle scar as well as the relative length of the ventral median septum, the relative length and width of the cardinalia, the relative length of the dorsal submedian septa and the relative width of the elevated, tuberculate areas, disposed as a pair of arcs on either side of the submedian septa, which almost certainly gave support to a schizolophous lophophore in *Sowerbyella*; the relevant statistics are given in Tables 82-90. The samples from the Lower Allt Ddu and the Upper Glyn Gower and Nant Hir Groups did not differ from each other in any aspect of relative growth and in view of other morphological comparisons they may be taken as samples drawn from the same population. Consequently the older, larger sample alone was used for the definition of the new subspecies and was employed in this capacity for comparisons with other stocks.

In all, 20 out of 42 tests of significance showed important differences ( $p$  varying from .05 to .001) between any two samples either in the growth ratio ( $a$  or  $\alpha$ ) of two attributes or in indices of inherent or residual shape ( $b$  or  $\beta$ ). The inter-relationships are complicated but when the results are assembled in a matrix table as in Text-fig. 12, the distinguishing features of the various taxa are soon appreciated. Hence, apart from the significantly finer radial ornamentation of the new species and subspecies and the dominantly subcarinate aspect of the pedicle valves of *S. soudleyensis*, it can be seen that :

(1) *S. musculosa* is unique in the inherently greater length relative to width of the ventral muscle field; the inherently longer socket ridges relative to the length of the brachial valve and in the relatively slower anterior extension of the submedian septa in the brachial valve.

(2) *S. musculosa* and *S. soudleyensis* differ from *S. sericea* (s.l.) in the relatively faster forward growth of the ventral septum and from *S. sericea* (s.s.) in the faster growth in length relative to width of their pedicle valves.

(3) *S. musculosa* and *S. sericea permixta* differ from *S. sericea* and *S. soudleyensis* in their socket ridges being inherently longer relative to their width.

(4) *S. soudleyensis* differs from *S. sericea* in the inherently greater depth of the pedicle valve relative to length.

It may be premature to derive any conclusions on the evolution of south British *Sowerbyella* from these comparisons but bearing in mind the stratigraphical context of the various stocks, it is probably significant that *S. sericea permixta* is the oldest and also the most generalized form. The new subspecies, for example, is a suitable ancestor for both *S. soudleyensis* and *S. sericea* but, although it is morphologically closer to the latter species, the former is more likely to be its contemporary. Furthermore, *S. musculosa* is decisively distinct from all other stocks in at least the three same features so that even if, on balance, it is morphologically nearer to the new subspecies, it is most probably an intrusive element appearing briefly within the faunal assemblages of the Anglo-Welsh basin. In view of these anomalies therefore, it is unlikely that the Caradocian forms of *Sowerbyella* present a simple picture of direct descent.



Genus *EOPLECTODONTA* Kozłowski 1929

TYPE SPECIES. *Sowerbyella praecursor* Jones by original designation of Kozłowski (1929 : 112).

*Eoplectodonta* cf. *rhombica* (M'Coy)

(Pl. 12, figs. 9-14, 18, 19)

1852 *Leptaena sericea* var. *rhombica* M'Coy : 239.

1928 *Sowerbyella rhombica* (M'Coy) Jones : 426-430, pl. 22, fig. 1.

DIAGNOSIS. Semi-circular to subquadrate *Eoplectodonta* with evenly concavo-convex longitudinal profile, rectimarginate or rarely faintly paraplicate anterior commissure and slightly acute to slightly obtuse cardinal angles in adult shells, pedicle valve about one-half as long as wide and over one-third as deep as long ; radial ornamentation consisting of unequally developed parvicostellae segregated into sectors about 1 mm. wide and with counts of 8 to 10 costellae per mm., 10 mm. antero-medially of ventral umbo, postero-lateral areas, also ornamented by rugae, with wavelength of over 0.25 mm. disposed acutely to hinge-line and commonly forming 10 or 11 pairs extending antero-medially through sectors of up to 30°; pseudodeltidium and chilidium small, apical ; teeth elongate, divergent dental lamellae obsolescent, denticles, about 3 to 4 per mm. commonly developed for over one-half the length of hinge-line lateral to teeth, but rarely throughout entire length ; ventral muscle field divided and deeply cordate in outline about three-quarters as long as wide and extending anteriorly for about one-half the length of pedicle valve, adductor scars small lanceolate, separated by median septum extending anteriorly for over one-half the length of field and deeply inserted posteriorly into callist beneath pseudodeltidium, diductor scars widely separated anteriorly and divided by divergent *vascula media* giving rise to lemniscate pallial sinus pattern ; cardinalia more than one-third as long as wide and consisting of strong high median cardinal process protruding ventrally of hollowed notothyrial platform and fused with chilidial plates and widely divergent socket ridges, median ridge strong and high, arising later than submedian septa but becoming ankylosed with them in adult valves, septa extending anteriorly for nearly three-fifths the length of brachial valve and flanked by pair of subpetaloid, elevated "lophophore platforms" divided by *vascula myaria* and about seven-tenths as long as wide ; pallial sinus pattern lemniscate.

| MATERIAL (Figured).                                      | length | width (mm.) |
|----------------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.29122)            | 13.5   | 22.0        |
| Incomplete internal mould of<br>pedicle valve (BB.29123) | 9.0    | —           |
| Deformed external mould of pedicle<br>valve (BB.29125)   | 9.0    | 15.5        |
| Incomplete external mould of<br>pedicle valve (BB.29126) | —      | —           |



| MATERIAL (Figured) ( <i>continued</i> ).               | length | width (mm.) |
|--------------------------------------------------------|--------|-------------|
| Deformed external mould of brachial valve (BB.29127)   | 8.0    | —           |
| Incomplete internal mould of brachial valve (BB.29128) | 11.5   | —           |
| Deformed internal mould of brachial valve (BB.29129)   | 8.0    | —           |
| Deformed internal mould of brachial valve (BB.29130)   | —      | —           |

HORIZON AND LOCALITIES. Gelli-grŷn Group : BB.29122, BB.29128, BB.29130 from calcareous ashes exposed at the south edge of wood, 850 ft. west of Gelli-grŷn Farm ; BB.29126-27 from calcareous ashes along the north side of track leading west from Gelli-grŷn Farm and 1,000 ft. west-south-west of the farm ; BB.29123, BB.29125, BB.29129, from calcareous ash quarry beside the drive to Y Garnedd Farm.

DISCUSSION. The complications that arise in restricting M'Coy's specific name *Eoplectodonta rhombica* to fossils from one locality have been adequately dealt with by Jones (1928 : 426-430) and do not require reiteration. Indeed, as a result of his investigations, the lectotype for the species is now a poorly preserved pedicle valve from the "Bala Limestone of Horton in Ribblesdale" (Jones 1928 : 427). According to King & Wilcockson (1934 : 11) the specimen was collected from the Crag Hill Beds which are now believed to be low Ashgillian in age (King & Williams 1948 : 207) an opinion confirmed by Dr. W. T. Dean in correspondence. Unfortunately, no good collection of topotypic material of *E. rhombica* was available for examination by the writer. But a few moulds of an *Eoplectodonta* from the *Calymene* Beds of Sally Beck, which is probably conspecific with *E. rhombica* (s.s.), showed no important differences from the Bala sample, except possibly for being relatively longer and less rugate. These differences, however, cannot at present be employed to distinguish between the two stocks because some of the Bala shells are similar to the Ashgillian moulds in outline and the suppression of rugation, and until we are in a position to assess the variability of both forms they must be considered conspecific irrespective of the difference in age.

As far as the Welsh shells are concerned, most of the relevant data are given in the diagnosis and in Tables 93-96. The pedicle valves are generally evenly convex, with only a faint paraplication antero-medially in 7 out of 20 valves, and a mean percentage depth relative to length of 37.3 (variance 113.73) in 9 pedicle valves between 4 and 12.5 mm. long. The parvicostellate radial ornamentation is rather finely developed with counts of 6, 7, 8, 9, 10 and 11 costellae per mm., 10 mm. antero-medially of the umbones of 1, 4, 14, 34, 15 and 5 pedicle valves ; at this distance from the ventral umbo thickened costellae divide the pattern into well defined segments with an average width of 1.0 mm. (variance 0.042) in 39 specimens. The rugae are also characteristic. They occupy up to 30° sectors in the postero-lateral areas in an interrupted concentric pattern which begins at 1 to 2 mm. from



the umbo and subtends acute angles with the hinge-line. For 31 specimens the average wavelength was 0.27 mm. (variance 0.0015) and 9, 10, 11, 12, 13, 14 and 15 rugae were counted along the right hinge lines of 2, 4, 3, 4, 1, 2 and 1 pedicle valves.

Internally the most interesting feature is the development of the triseptate condition of the brachial valve because like the American and Scottish species (see Williams 1962 : 184) the median ridge develops after the submedian septa that form the inner boundaries to the lophophore platform. In 7 out of 9 of the smallest brachial valves, with the submedian septa up to 2.9 mm. long, the median ridge is seen to have developed later than the diverging submedian septa ; in the remaining 2 specimens no ridge occurred. This condition persisted in some specimens so that the ridge was also absent in 4 out of 12 specimens with submedian septa up to 5.9 mm. long. But in 2 out of 8 specimens with longer submedian septa, excessive secretion of secondary shell about the ridge caused it to fuse posteriorly with the notothyrial platform and so to dominate the median region of the valve as an eminence raised above the level of the submedian septa.

TABLE 93

|                        |   |   |       |           |
|------------------------|---|---|-------|-----------|
| $\bar{l}$ mm. (var. l) | . | . | 6.1   | (5.868)   |
| $\bar{w}$ mm. (var. w) | . | . | 12.1  | (23.407)  |
| r                      | . | . | 0.966 |           |
| a (var. a)             | . | . | 1.997 | (0.01025) |

TABLE 93. Statistics of length (l) and maximum width (w) of 28 pedicle valves of *Eoplectodonta* cf. *rhombica* (M'Coy).

TABLE 94

|                          |   |   |       |           |
|--------------------------|---|---|-------|-----------|
| $\bar{l}$ mm. (var. l)   | . | . | 7.5   | (7.719)   |
| $\bar{sc}$ mm. (var. sc) | . | . | 3.8   | (2.352)   |
| r                        | . | . | 0.832 |           |
| a (var. a)               | . | . | 0.552 | (0.00446) |

TABLE 94. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 23 specimens of *Eoplectodonta* cf. *rhombica* (M'Coy).

TABLE 95

|                                     |   |   |        |           |
|-------------------------------------|---|---|--------|-----------|
| $\bar{l}$ mm. (var. l)              | . | . | 3.3    | (1.409)   |
| $\bar{w}$ mm. (var. w)              | . | . | 4.3    | (1.405)   |
| r                                   | . | . | 0.903  |           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | . | 1.1228 | (0.1239)  |
| $\log_e \bar{w}$ (var. $\log_e w$ ) | . | . | 1.4168 | (0.0744)  |
| $r_e$                               | . | . | 0.910  |           |
| $\alpha$ (var. $\alpha$ )           | . | . | 0.7749 | (0.00685) |

TABLE 95. Statistics of length (l) and maximum width (w) of the ventral muscle scar of 17 pedicle valves of *Eoplectodonta* cf. *rhombica* (M'Coy).



TABLE 96

|                |   |   |        |           |
|----------------|---|---|--------|-----------|
| l mm. (var. l) | . | . | 6.4    | (6.57)    |
| s mm. (var. s) | . | . | 3.8    | (2.216)   |
| r              | . | . | 0.927  |           |
| a (var. a)     | . | . | 0.5808 | (0.00237) |

TABLE 96. Statistics of length of brachial valve (l) and length of submedian septa (s) for 22 specimens of *Eoplectodonta* cf. *rhombica* (M'Coy).

Between 8 and 21 denticles occurred along the right hinge-lines of 14 specimens but in only one valve did denticles occupy the entire hinge-line; mostly they occupied between one-third and three-quarters of the hinge-line with an average of just over one-half for 7 specimens.

*E. cf. rhombica* is clearly quite distinct from *E. acuminata* (Holtedahl 1916) emended Spjeldnaes (1956 : 96), *E. semirugata* (Reed 1917) emended Williams (1962 : 181) and *E. lenis* Williams (*In* Whittington & Williams 1955 : 417) at least in the much greater concavo-convexity of its profile. At the same time it is different from *E. conspicua* (Reed 1917) emended Williams (1962 : 182), to which it has frequently been compared (Jones 1928 : 431), in lacking the carination of the pedicle valve and in having a significantly greater relative width due to the faster anterior growth of the Scottish shells.

#### Genus **SERICOIDEA** Lindström 1953

TYPE SPECIES. *Leptaena sericea* var. *restricta* Hadding by original designation of Lindström (1953 : 134).

#### **Sericoidea** sp. (Pl. 12, figs. 15, 16)

A small number of poorly preserved *Sericoidea* have been collected from calcareous ashes of the Gelli-grîn Group exposed above the Limestone in the old quarries in Ffridd Bach, south of Maes-meillion Farm, and the casts of incomplete moulds of a dorsal interior (BB.29155) and a ventral exterior (BB.29156) have been figured to illustrate the chief characteristics of the species.

The shells were evidently gently concavo-convex in profile and semi-circular in outline and were ornamented by fine parvicostellae segregated into narrow segments by a thickening of every fifth or sixth costella and numbering about 12 per mm. at 2 mm. antero-medially of the ventral umbo. No interior of the pedicle valve is well enough preserved to show more than the obsolescence of the dental lamellae but the dorsal interior is sufficiently distinctive to indicate that the stock is quite different from other described species attributed to the genus. Thus, although the cardinalia were orthodoxly arranged with a high median cardinal process and a pair of widely divergent socket ridges, a well defined lophophore platform was built up in adult valves by the amalgamation of relatively long septa. The septa themselves, up to 17 in number, consisted of a strong median one, extending forward for about three-fifths the length of the valve, flanked by two sets of smaller ones



disposed in a pair of arcs. Each septum was highest and thickest at its anterior end and tended to fuse with its neighbours posteriorly so that a platform, deeply indented medianly and sharply crenulated peripherally, resulted.

The elaboration of a lophophore platform by the lateral fusion of a number of septa serves to distinguish the Gelli-grîn *Sericoidea* from *S. abdita* Williams which is known to occur in the Nant Hir Group (Whittington & Williams 1955 : 418). For in adult brachial valves of the latter species the median septum is flanked by only 3 pairs of discrete short septa arranged in arc. Even in the more advanced *S. restricta* (Hadding) from the Sulårp Shale of Sweden and the Craighead Limestones and Mudstones of Scotland (see Williams 1962 : 187-190), the arc defining the anterior of the lophophore platform consists of discrete septules and there is little doubt that the Gelli-grîn forms will prove to be specifically distinct when enough material is obtained to assess the variability of their morphology.

### Superfamily STROPHOMENACEA King 1846

#### Family STROPHOMENIDAE King 1846

#### Genus **STROPHOMENA** de Blainville 1825

TYPE SPECIES. *Strophomena rugosa* Rafinesque by subsequent designation of King (1846 : 28).

#### ***Strophomena grandis*** (J. de C. Sowerby)

(Pl. 12, figs. 17, 20, 21 ; Pl. 13, fig. 2)

1839 *Orthis grandis* J. de C. Sowerby : 638, pl. 20, figs. 12, 13.

1933 *Longvillia grandis* (J. de C. Sowerby) Bancroft : 3.

DIAGNOSIS (emended). Elongately semi-oval, gently convexo-concave *Strophomena* with pedicle valve about seven-tenths as long as wide slightly convex for about 3 mm. around the umbonal region but slightly and evenly concave in transverse and longitudinal profiles of adult valves, brachial valves about one-eighth as deep as long, cardinal angles slightly acute to rectangular, ventral interarea apsacline, pseudodeltidium small, foramen sealed at least in adult valves, dorsal interarea anacline, chilidium arched and only covering the dorsal ends of cardinal process lobes ; radial ornamentation strongly unequally parvicostellate with 4 costellae per mm., 10 mm. antero-medianly of ventral umbo and commonly with every third or fourth thickened to give narrow segments ; teeth small, obliquely disposed and fused with short dental lamellae subtending an angle of about 90° at apex, ventral muscle field commonly faintly impressed especially anteriorly, over two-fifths as long as pedicle valve and tending to be subcircular in young valves, but longer than wide in adult shells with submedian diductor lobes extending well beyond anterior limits of lanceolate adductor scar but not completely enclosing it ; ventral pallial sinus pattern probably digitate, *vascula media* subparallel dividing anteriorly ; cardinal process lobes, long, divergent with deeply concave posterior faces and ankylosed to widely divergent socket ridges, notothyrial platform



and median ridge faintly developed, dorsal adductor scars lightly impressed, obscure anteriorly but probably subtriangular and divided by at least two pairs of low divergent ridges ; dorsal pallial sinus pattern unknown.

|            |                                                                    | length | width (mm.) |
|------------|--------------------------------------------------------------------|--------|-------------|
| LECTOTYPE. | Internal mould of pedicle valve<br>(G.S.M., Geol. Soc. Coll. 6823) | 38.0   | 48.0        |
| OTHER      | Internal mould of brachial valve                                   |        |             |
| MATERIAL   | (G.S.M. Geol. Soc. Coll. 6897),                                    | 36.0   | —           |
|            | Incomplete external mould of<br>pedicle valve (BB.29150)           | 30.0   | —           |
|            | Incomplete external mould of<br>brachial valve (BB.29151)          | —      | —           |

HORIZON AND LOCALITIES. Marshbrookian Stage : G.S.M., G.S.C. 6823, G.S.M., G.S.C. 6897 from "Acton Scott"; BB.29150-51 from buff coloured sandstones exposed in the quarry in Marsh Wood.

DISCUSSION. It is clear from the fossils associated with the specimens described by Sowerby as *Orthis grandis* that they were originally taken from the *Dalmanella watti* beds of South Shropshire and, in redefining the species, only moulds recovered from this horizon have been used. Complete specimens are, however, comparatively rare so that not very much information on the variability of the stock can be provided. The shell is transversely semi-oval in outline with the greatest width at the hinge-line although a mucronate condition is unknown at least in adult stages of growth. The mean percentage length relative to width (with variance) for five pedicle valves between 10 and 30 mm. long was 71.6 (17.25). The radial ornamentation is typically strophomenid with counts of 4 costellae per mm. in six pedicle valves at a distance of 10 mm. antero-medially of the umbo. The lectotype (G.S.C. 6823) is an internal mould of a gerontic pedicle valve in which the ventral muscle field is exceptionally well defined and is elongately suboval in outline being about three-quarters as wide as long. In smaller pedicle valves, the anterior boundaries to the ventral muscle field are obscure and even when they are well seen, as in two valves 26 and 29 mm. long, they are subcircular in outline and about as wide as long. The accelerated anterior migration of the muscle field in late growth stages, however, must have been concomitant with a greater anterior growth of the shell, because in the lectotype and the two valves just mentioned the percentage length of the fields relative to that of the valves was 42, 44 and 44 respectively.

Bancroft (1933 : 3) proposed the genus *Longvillia* with *Strophomena grandis* as type species. In so doing he compared the genus with *Fardenia* Lamont, but made no reference at all to *Strophomena*. The omission is a curious one, unless he believed the "pecten-group" of shells to typify *Strophomena* because *S. grandis* is in no way generically separable from *S. planumbona* Hall and other typical members of that genus.



*Strophomena* sp.

(Pl. 13, figs. 1,3,4)

Incomplete external and internal moulds of a pedicle valve (BB.29062-63) recovered from sandstones of the Upper Allt Ddu Group exposed on the western side of Bryn Cut, about 50 ft. below the Pont-y-Ceunant Ash and 650 ft. east of Holy Trinity Church ; and an internal mould of a brachial valve (BB.28887) collected from calcareous ashes of the Gelli-grîn Group cropping out above the Gelli-grîn Limestone in the old quarries at Ffridd Bach, south of Maes-meillion have been figured to show the *Strophomena* that very rarely occurs in the highest Caradocian rocks of the Bala district. The pedicle valve, about 23 mm. long, was transversely semi-oval in outline with acute cardinal angles and evenly concave transverse and longitudinal profiles attaining a maximum depth of about one-sixth the length of the valve. The radial ornamentation was unequally parvicostellate with finely cancellated, closely packed, rounded costellae numbering 6 per mm., at 10 mm. antero-medially of the ventral umbo ; the interarea was apsacline, the pseudodeltidium well developed and the foramen small and supra-apical. Internally, the small teeth were supported by divergent dental lamellae extending anteriorly for about one-sixth the valve length ; and the subflabellate ventral muscle field was slightly wider than long and over two-fifths as long as the valve with a well developed, lanceolate and undifferentiated adductor scar, located postero-medially and enclosed by the lobate diductor scars. A conspicuous subperipheral rim of secondary shell, indented by pallial sinus furrows, occurred within 3-4 mm. of the valve margin.

The dorsal mould shows that the brachial valve which was about 17 mm. long, was also transversely semi-oval in outline, gently convex in profile, and similarly equipped with a subperipheral rim. The cardinal process lobes were small but conspicuous, ankylosed to a faint median ridge and to the widely divergent socket ridges ; the dorsal adductor scars were only vaguely impressed on either side of the median ridge about two pairs of divergent, low ridges.

The species is clearly related to *Strophomena grandis* J. de C. Sowerby but differs from it, at least in being more highly convexo-concave and more finely ornamented and in the subquadrate outline of the ventral muscle scar. These differences will probably prove to be significant but until more material is obtained to assess the variability of these and other features it is better to withhold taxonomic recognition.

Genus *GLYPTOMENA* Cooper 1956

TYPE SPECIES. *Glyptomena sculpturata* Cooper by original designation of Cooper (1956 : 881).

*Glyptomena* cf. *osloensis* (Spjeldnaes)

(Pl. 13, figs. 5, 6, 8, 9)

DESCRIPTION. Subquadrate, strongly concavo-convex *Glyptomena* ornamented postero-laterally by 3 or 4 pairs of short rugae with a wavelength of about 1 mm.



disposed at a slightly acute angle to the hinge-line and extending forwards through a 35° sector of the shell surface, radial ornamentation consisting of unequal, rounded, parvicostellae well differentiated into segments up to 1.5 mm. thick and numbering about 5 per mm., 10 mm. antero-medially of the ventral umbo ; pseudodeltidium small or lacking, chilidium large, strongly convex ; teeth large, pustulose, continuous with widely divergent, short dental lamellae, ventral muscle scar subrhomboidal in outline, adductor scars lanceolate, separated by a faint median ridge and about one-half as long as the slightly divergent, submedian diductor lobes ; dorsal interior imperfectly preserved, notothyrial platform short, three-pronged with the lateral extensions fused with wide-splayed socket ridges, adductor impressions contained posteriorly between the median and lateral prongs and divided by a pair of slightly divergent low ridges.

**MATERIAL** (Figured). One internal and two external moulds of pedicle valves (BB.29101-03). Fragment of internal mould of brachial valve (BB.29104).

**HORIZON AND LOCALITY.** Gelli-grîn Group : all specimens from calcareous ashes immediately west of deep, overgrown quarry, 1,450 ft. east-north-east of Y Garnedd Farm.

**DISCUSSION.** A few moulds, taken from the Gelli-grîn Group, are evidently representative of the genus *Glyptomena* Cooper (see Williams 1962 : 210) and compare closely with *G. osloensis* (Spjeldnaes 1957 : 161-167) from stage 4b $\alpha$  of Norway. There are, however, some differences, notably the rounded geniculate profile of the Norwegian shells, but this is not greatly different from the very strong convexity of the Welsh specimens and until more is known about the variability of the latter it is feasible to treat the stocks as conspecific.

### Genus *MACROCOELIA* Cooper 1956

**TYPE SPECIES.** *Macrocoelia obesa* Cooper by original designation of Cooper (1956 : 890).

#### *Macrocoelia expansa* (J. de C. Sowerby)

(Pl. 13, figs. 7, 10-14 ; Pl. 14, figs. 1, 2, 5 ; Text-fig. 13)

1839 *Strophomena expansa* J. de C. Sowerby : 638, pl. 20, fig. 14.

1871 *Strophomena expansa* Sowerby ; Davidson : 312 *pars*, pl. 45, figs. 1, 6, 8, 10, *non* figs. 2-5, 7, 9.

**DIAGNOSIS** (emended). Elongately subquadrate to semi-oval, concavo-convex *Macrocoelia* with evenly convex pedicle valve almost four-fifths as long as wide and almost one-eighth as deep as long, cardinal angles slightly obtuse to slightly acute ; radial ornamentation strongly unequally parvicostellate, finely cancellate and tending to curve outwards posterolaterally with counts of 4 or 5 costellae per mm., at 10 mm. anterior of ventral umbo and commonly with every third or fourth



costella thickened to give a narrowly segmented appearance ; 3 to 5 impersistent rugae commonly developed postero-laterally disposed at acute angles to hinge-line and extending antero-medianly through a sector of about  $20-25^{\circ}$  in each postero-lateral area ; ventral interarea apsacline, delthyrium relatively narrow, pseudo-deltidium absent in adult shells, dorsal interarea anacline, chilidium large and convex ; teeth small, elongated and ankylosed with widely divergent dental lamellae to form pair of hollow, acutely triangular structures extending anteriorly for about one-twelfth the length of pedicle valve ; ventral muscle field large, splayed, subcircular extending anteriorly for about one-half the length of pedicle valve and about four-fifths as long as wide with elevated radiating ridges separating each diductor scar into as many as 5 distinct lobes in adult shells, pedicle callist well developed, passing into broad, medianly indented ridge extending anteriorly for about one-seventh the length of pedicle valve, adductor scars lanceolate, commonly indistinct and impressed anterior of ridge ; cardinal process lobes with splayed posterior faces, not greatly elevated above anchor-shaped notothyrial platform, median septum between lobes commonly vestigial ; socket ridges elongate and ankylosed to lateral extensions of notothyrial platform, dorsal adductor impressions vague, divided by pair of narrowly divergent ridges ; ventral pallial sinus pattern saccate with up to 4 pairs of arcuate branches arising from subjacent *vascula media* ; dorsal pattern unknown.



FIG. 13. The ventral internal mould of *Macrocoelia expansa* (J. de C. Sowerby),  $\times 2.5$  approx., showing the pallial sinus pattern : gg, *vascula genitalia* ; m, *vascula media*.



|            |                                                                            | length | width (mm.) |
|------------|----------------------------------------------------------------------------|--------|-------------|
| LECTOTYPE. | Incomplete internal mould of pedicle valve (G.S.M., Geol. Soc. Coll. 6863) | —      | —           |
| OTHER      |                                                                            |        |             |
| MATERIAL.  | Incomplete internal mould of brachial valve (BB.29112)                     | —      | —           |
|            | Incomplete internal mould of pedicle valve (BB.29113)                      | —      | —           |
|            | External mould of pedicle valve (BB.29114)                                 | 17·0   | —           |
|            | Internal mould of pedicle valve (BB.29115)                                 | 37·0   | 43·0        |
|            | Internal mould of pedicle valve (BB.29116)                                 | 17·0   | 22·0        |
|            | Incomplete internal mould of brachial valve (BB.29117)                     | —      | —           |
|            | External mould of pedicle valve (BB.29118)                                 | 39·0   | 46·0        |
|            | External mould of pedicle valve (BB.29119)                                 | —      | —           |

HORIZON AND LOCALITY. Lower Longvillian Substage : lectotype G.S.M., G.S.C. 6863 from " Caradoc Sandstone, Meifod ", Montgomeryshire ; all other specimens from siltstones exposed on Gallt-yr-ancr, 440 yds. north of west from Dyffryn, one-half mile south-west of Meifod Church.

***Macrocoelia prolata* sp. nov.**

(Pl. 14, figs. 3, 4, 6-10)

DIAGNOSIS. Elongately semi-oval, concavo-convex *Macrocoelia* with evenly convex pedicle valve over four-fifths as long as wide and less than one-fifth as deep as long, cardinal angles slightly obtuse to slightly acute ; radial ornamentation strongly unequally parvicostellate, finely cancellate and curving outwards postero-laterally, with counts of 6 or 7 costellae per mm., at 10 mm. anterior of ventral umbo and commonly with every third or fourth costella thickened to give a narrowly segmented appearance ; about 8 impersistent rugae developed postero-laterally, disposed at acute angles to hinge-line and extending antero-medianly through a sector of about 45° in each postero-lateral area ; ventral interarea apsacline, delthyrium relatively narrow, pseudodeltidium absent in adult shells, dorsal interarea anacline, chilidium large and convex ; teeth small, elongated and ankylosed with widely divergent dental lamellae to form pair of hollow acutely triangular structures extending anteriorly for about one-tenth the length of pedicle valve ; ventral muscle field large, splayed, subcircular in outline, extending anteriorly for less than one-half the length of pedicle valve and about nine-tenths as long as wide with elevated radiating ridges separating each diductor scar into as many as 5 distinct



lobes in adult shells, pedicle callist well developed, passing into broad, medianly indented ridge extending anteriorly for about one-seventh the length of pedicle valve, adductor scars indistinct ; posterior faces of cardinal process lobes not greatly splayed or elevated above anchor-shaped notothyrial platform, median septum between lobes commonly vestigial ; socket ridges elongate and ankylosed to lateral extensions of notothyrial platform, dorsal adductor scars vaguely impressed and divided by pair of narrowly divergent ridges ; pallial sinus patterns unknown.

|            |                                                        | length | width (mm.) |
|------------|--------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | External mould of pedicle valve (BB.29106)             | —      | 25.0        |
| PARATYPES. | External mould of pedicle valve (BB.29107)             | 9.5    | 12.5        |
|            | External mould of pedicle valve (BB.29105)             | 16.5   | 20.0        |
|            | Internal mould of pedicle valve (BB.29108)             | 10.0   | 11.5        |
|            | Incomplete internal mould of pedicle valve (BB.29109)  | —      | —           |
|            | Incomplete internal mould of brachial valve (BB.29110) | —      | —           |
|            | Incomplete internal mould of brachial valve (BB.29111) | —      | —           |

HORIZON AND LOCALITY. Allt Ddu Group : BB.29105 from crags of fine sandstones and mudstones, 1,100 ft. south-west of Eglwys Anne ; BB.29106–11 from fine sandstones underlying the Pont-y-Ceunant Ash and exposed north of the drive to Y Garnedd Farm.

DISCUSSION. The species *Strophomena expansa* J. de C. Sowerby is a well known but inadequately defined stock that has been widely identified in Caradocian rocks from a number of localities throughout Britain (see Davidson 1871 : 314). There is, however, no doubt that when Sowerby erected the species, he had in mind the strophomenids occurring abundantly and in association with *Howellites antiquior* (M'Coy) in fine, blue-grey sandstones exposed in the vicinity of Meifod (see Whittington 1938 : 428–431). Accordingly, a good sample, taken from exposures on Gallt-yr-ancr, has been used to provide a revised description of the species which is also now recognised as belonging to the genus *Macrocoelia*.

*Macrocoelia* also occurs sporadically in the Allt Ddu Group of the Bala district. It is commonest in the ashy sandstone members towards the top of the formation and, although related to *M. expansa*, a sample from this horizon has proved to be distinct in a sufficient number of features to merit taxonomic recognition. In shell outline and profile (Tables 97, 100) there is no important difference between the two species because although the pedicle valves of the new species tend, on an average, to be relatively longer and deeper the discrepancies are covered by the variability of the samples. The surface ornamentation of the new species however, is quite



distinctive. Counts of 3, 4, 5, 6, 7 and 8 costellae per mm. at a distance 10 mm. antero-medially of the ventral umbo, were obtained in 0, 0, 0, 4, 9 and 2 pedicle valves of the new species compared with 5, 10, 15, 6, 1 and 0 valves of *M. expansa*; the differences are highly significant ( $p < .001$ ). In both species, rugae with a wavelength of 0.5 mm. are disposed at acute angles to the hinge-line but they are longer in the new species extending antero-medially through  $45^\circ$  sectors of the postero-lateral areas compared with  $20-25^\circ$  sectors in *M. expansa*. The rugae are also more numerous and persistent in the new species because they have been seen on every external mould examined and 7, 8, 9 and 10 have been counted on the right sides of 1, 5, 2 and 2 pedicle valves compared with 2, 3, 4, 5, 6, 7 and 8 on the right sides of 2, 10, 7, 6, 1, 5 and 3 pedicle valves of *M. expansa* with no rugae developed at all in a further 15 valves.

TABLE 97

|                                     | A |                  | B |                 |
|-------------------------------------|---|------------------|---|-----------------|
| $\bar{l}$ mm. (var. l)              | . | 22.9 (123.987)   | . | 10.2 (29.853)   |
| $\bar{w}$ mm. (var. w)              | . | 28.9 (189.979)   | . | 12.0 (34.304)   |
| r                                   | . | 0.989            | . | 0.993           |
| $\log_e \bar{l}$ (var. $\log_e l$ ) | . | 3.0248 (0.2126)  | . | 2.1917 (0.2533) |
| $\log_e \bar{w}$ (var. $\log_e w$ ) | . | 3.2618 (0.2053)  | . | 2.3765 (0.2167) |
| $r_e$                               | . | 0.987            | . | 0.993           |
| $\alpha$ (var. $\alpha$ )           | . | 0.9827 (0.00113) | . | 0.925 (0.0008)  |

TABLE 97. Statistics of length (l) and maximum width (w) of 24 pedicle valves of *Macrocoelia expansa* (J. de C. Sowerby) (A) and of 17 pedicle valves of *M. prolata* sp. nov. (B).

TABLE 98

|                                       | A |                 | B |                 |
|---------------------------------------|---|-----------------|---|-----------------|
| $\bar{l}$ mm. (var. l)                | . | 28.7 (66.131)   | . | 23.5 (75.625)   |
| $\bar{sc}$ mm. (var. sc)              | . | 14.6 (19.933)   | . | 11.4 (30.519)   |
| r                                     | . | 0.958           | . | 0.974           |
| $\log_e \bar{l}$ (var. $\log_e l$ )   | . | 3.2779 (0.078)  | . | 3.0928 (0.1283) |
| $\log_e \bar{sc}$ (var. $\log_e sc$ ) | . | 2.6353 (0.09)   | . | 2.3243 (0.2118) |
| $r_e$                                 | . | 0.954           | . | 0.984           |
| a (var. a)                            | . | 1.074 (0.00334) | . | 1.285 (0.00748) |

TABLE 98. Statistics of length of pedicle valve (l) and length of ventral muscle scar (sc) for 33 specimens of *Macrocoelia expansa* (J. de C. Sowerby) (A) and for 9 specimens of *M. prolata* sp. nov. (B).

TABLE 99

|                        | A |                | B |                 |
|------------------------|---|----------------|---|-----------------|
| $\bar{l}$ mm. (var. l) | . | 15.3 (14.893)  | . | 10.6 (12.77)    |
| $\bar{w}$ mm. (var. w) | . | 18.2 (22.063)  | . | 11.4 (16.968)   |
| r                      | . | 0.934          | . | 0.997           |
| a (var. a)             | . | 1.217 (0.0051) | . | 1.153 (0.00159) |

TABLE 99. Statistics of length (l) and maximum width (w) of the ventral muscle scars of 39 pedicle valves of *Macrocoelia expansa* (J. de C. Sowerby) (A) and of 7 pedicle valves of *M. prolata* sp. nov. (B).



TABLE 100

|                  |   |   |        |           |
|------------------|---|---|--------|-----------|
| l mm. (var. l)   | . | . | 11.6   | (37.445)  |
| th mm. (var. th) | . | . | 2.1    | (1.379)   |
| r                | . | . | 0.946  |           |
| a (var. a)       | . | . | 0.1919 | (0.00035) |

TABLE 100. Statistics of length (l) and maximum depth (th) of 13 pedicle valves of *Macrocoelia prolata* sp. nov.

The only known internal differences relate to the relative length of the ventral muscle scars. In both species the muscle scars are subcircular and splayed and only slightly wider than long (Table 99) with well developed postero-median ridges. The ridges have a mean percentage length relative to the length of 9 pedicle valves of *M. expansa*, between 18 and 37 mm. long, of 13.5 (variance 3.095) compared with 14.1 for 3 pedicle valves of *M. prolata*. There is however an important difference in the anterior advance of the ventral muscle field because although the scars of the Bala species were, on an average, only slightly shorter, relative to the length of the pedicle valves, than those of *M. expansa*, they were inherently so; and a comparison of the growth rates, (Table 98), shows that the scars of the new species expanded anteriorly at a significantly faster rate ( $p < .05$ ).

In summary then, the new species differs from *M. expansa* in its finer radial ornamentation, in the invariable presence of more numerous and longer rugae and in the relatively faster anterior migration of the ventral muscle scar: and in respect of these features other, rarer *Macrocoelia* collected from older rocks in the Bala district are clearly related to *M. prolata* rather than *M. expansa*.

### Genus *HEDSTROEMINA* Bancroft 1929

TYPE SPECIES. *Hedstroemina fragilis* Bancroft by original designation of Bancroft (1929: 56).

#### *Hedstroemina* ? spp.

(Pl. 14, figs. 11, 12)

Two internal ventral moulds (BB.29120-21) of a rafinesquinid stock have been collected respectively from siltstones of the Glyn Gower Group exposed as crags in the wood immediately east of Cefn-bodig and from mudstones of the Nant Hir Group cropping out on the left bank of the Nant Hir, 600 ft. north-east of Cefn-y-maes Farm and are the only specimens known from the post-Derfel Limestone rocks of the Bala district that can be referred to either *Kjaerina* Bancroft (1929) or *Hedstroemina* Bancroft (1929). The mould from the Glyn Gower rocks (BB.29120) is of an elongately oval, evenly convex pedicle valve, about 11 mm. long and over one-quarter as deep as long with small, thin, divergent dental lamellae extending anteriorly for less than one-tenth the length of the valve. The muscle field appears to have been small but the impressions are indistinct; the radial ornamentation is impressed towards the margin and shows that the pattern was an unequally parvicostellate one with about 7 costellae per mm., at 10 mm. antero-medianly of the umbo.



The other mould (BB.29121), which is 12 mm. long, is quite different in outline and profile for it represents a transversely oval pedicle valve about three-quarters as long as wide and less than one-fifth as deep as long, although it, too, is characterized by fragile, moderately divergent dental lamellae, obscure muscle impressions and peripherally impressed, unequally developed parvicostellae with about 6 costellae per mm. antero-medianly.

It is possible that these two specimens represent two distinct species but at present even their generic identification is in doubt. Thus the Nant Hir specimen is reminiscent of *Hedstroemina parva* (Bancroft 1929 : 57, pl. 2, fig. 5) whereas the Glyn Gower mould is very like *Kjaerina horderleyensis* (Bancroft 1929 : 50, pl. 1, fig. 12) a form that lacks the strong median rib so typical of *Kjaerina*. Indeed it is only the absence of this feature that has prompted the provisional allocation of both specimens to *Hedstroemina* ; more material might show the stocks to be *Kjaerina* which is characterized by equally generalized ventral internal features.

Family LEPTAENIDAE Cooper 1956

Genus **LEPTAENA** Dalman 1828

TYPE SPECIES. *Leptaena rugosa* Dalman by subsequent designation of King (1846 : 28).

***Leptaena salopiensis* sp. nov.**

(Pl. 15, figs. 7, 8, 10-16)

DIAGNOSIS. Concavo-convex, strongly geniculate *Leptaena* with disc surrounded by prominent, ventral fold with wavelength of 2-3 mm. and complementary dorsal trench, disc transversely quadrate, about 13 mm. long, just over three-fifths as long as wide and with ventral depth of about one-sixth the length due to strongly convex ventral umbo, trail bent back sharply at about 100° to give an overall depth of about two-fifths the length of adult pedicle valves ; radial ornamentation parvicostellate and not well differentiated into segments, commonly with 4 rounded costellae per mm., 10 mm. antero-medianly of ventral umbo ; 5 or 6 concentric and rarely discontinuous rugae, with wavelength of about 1.5 mm. in later ones also ornament the disc ; pseudodeltidium small, foramen small, commonly sealed in adult shells, chilidium large, convex and commonly bearing slight median depression ; teeth obliquely splayed and fused with widely divergent short dental lamellae, ventral muscle scar elongately rhomboidal in outline, nearly nine-tenths as wide as long and extending anteriorly for nearly three-quarters the length of disc in adult shells, adductor scars small, lanceolate separated posteriorly by low median ridge extending from low median platform occupying delthyrial floor, submedian diductor lobes extending well beyond adductors but not enclosing them ; cardinal process lobes slender and commonly separated by faint median ridge, notothyrial platform anchor-shaped with short median stem and strongly curved lateral ridges fused with socket ridges and enclosing posteriorly the subcircular adductor impressions ; a pair of curved submedian ridges originate near median prolongation of notothyrial platform to divide adductor impressions and converge anteriorly commonly to contain anterior median ridge.



|            |                                                                         | length | width (mm.) |
|------------|-------------------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | External and internal mould of pedicle valve (BB.29144-45)              | 20.0   | 29.0        |
| PARATYPES. | External and internal moulds of pedicle valve (BB.29136-37)             | 16.0   | 25.0        |
|            | External and internal moulds of pedicle valve (BB.29138-39)             | 17.0   | 31.0        |
|            | External and internal moulds of brachial valve (BB.29140-41)            | 13.0   | —           |
|            | Incomplete external and internal moulds of brachial valve (BB.29142-43) | —      | —           |

HORIZON AND LOCALITY. Actonian Stage : all specimens from loose blocks near Acton Scott Church, possibly from the quarry of Castle Hill, one-third of a mile west-south-west of Acton Scott.

*Leptaena ventricosa* sp. nov.

(Pl. 15, figs. 1-6, 9)

DIAGNOSIS. Concavo-convex, strongly geniculate *Leptaena* with disc surrounded by prominent fold with wavelength of 2-3 mm., disc transversely quadrate, about 9 mm. long, just over three-fifths as long as wide and with ventral depth of about one-fifth the length due to strongly convex ventral umbo, trail bent back sharply at about 90° to give an overall depth of about one-half the length of pedicle valve ; radial ornamentation parvicostellate and not well differentiated into segments, commonly with 4 rounded costellae per mm., 10 mm. antero-medianly of ventral umbo ; 8 or 9 concentric and rarely discontinuous rugae, with wavelength less than 1 mm., in later formed ones also ornament disc ; pseudodeltidium small, foramen small, commonly sealed in adult shells, chilidium large, convex and commonly bearing slight median depression ; teeth large, strongly striated, obliquely splayed and fused with widely divergent short dental lamellae, ventral muscle scar elongately rhomboidal in outline, nearly nine-tenths as wide as long and extending anteriorly for nearly three-quarters the length of disc in adult shells, adductor scars small, lanceolate, separated posteriorly by low median ridge extending from low median platform occupying delthyrial floor, submedian diductor lobes extending well beyond adductors but not enclosing them ; cardinal process lobes well developed, high and separated by faint median ridge, sockets striated, notothyrial platform anchor-shaped with short median stem and strongly curved lateral ridges fused with socket ridges and enclosing posteriorly the subcircular adductor impressions ; a pair of curved submedian ridges originate near median prolongation of notothyrial platform to divide adductor impressions and converge anteriorly commonly to contain anterior median ridge.



|            |                                                                        | length | width (mm.) |
|------------|------------------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Incomplete external and internal mould of brachial valve (BB.29044-45) | —      | —           |
| PARATYPES. | External mould of pedicle valve (BB.29042)                             | 10.0   | —           |
|            | Deformed internal mould of brachial valve (BB.29043)                   | 11.0   | —           |
|            | Deformed internal mould of pedicle valve (BB.29041)                    | —      | —           |
|            | Incomplete internal mould of brachial valve (BB.29046)                 | —      | —           |
|            | Deformed internal mould of pedicle valve (BB.29047)                    | 15.0   | —           |
|            | External mould of pedicle valve (BB.29048)                             | —      | —           |

HORIZON AND LOCALITIES. Gelli-grŷn Group : BB.29042, BB.29044-45, from ashy mudstones exposed on the right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern Farm ; BB.29041, BB.29047 from calcareous ash crags immediately west of the fence, 1,100 ft. just south of west of Gelli-grŷn Farm ; BB.29043 from calcareous ash scarp immediately east of wall and 150 ft. north of sheepfold, 2,600 ft. east of Pont-y-onen Farm ; BB.29046 from calcareous ashes before the Rhiwlas Limestone scarp on the north side of the northern outlier on Creigiau Bychain ; BB.29048 from calcareous ash exposures west of the track on the north-east side of the central outlier of Rhiwlas Limestone on Creigiau Bychain.

DISCUSSION. These two new species, representatives of which are fairly common in the ashes and limestones of the Gelli-grŷn Group and in mudstones and sandstones of the Actonian Stage are the only examples of *Leptaena*, as understood by Spjeldnaes (1957 : 171), so far recorded from the Caradocian rocks of south Britain. Externally the most distinctive feature is undoubtedly the raised rim surrounding the ventral surface of the disc and representing a sharp, rounded, ventrally directed fold in the zone of geniculation. The average length of the disc in 20 pedicle valves of *L. ventricosa* was 9.2 mm. (variance 1.53) and its average percentage length relative to width in 4 pedicle valves was 63 (range 57-66). The values for 37 and 16 pedicle valves of *L. salopiensis* were respectively 13.0 mm. (1.757) and 62.4 (variance 70.47), and it is clear that in spite of similar outlines the disc of the Shropshire species is absolutely longer ( $p < .001$ ). There is also an important difference in ornamentation. The parvicostellate pattern is fairly coarse in both species with no conspicuous differential thickening of rounded costellae to define segments and 3, 4, 5 and 6 costellae per mm. were counted at 10 mm. antero-medially of the umbo in 1, 7, 1 and 0 pedicle valves of *L. ventricosa* and 6, 17, 6 and 1 of *L. salopiensis*. The rugae, which are more or less symmetrical, are not invariably continuous in their concentric disposition because the earlier formed ones in particular may be interrupted by



saddles here and there. There is, however, a significant difference ( $p < 0.01$ ) in the number of rugae displayed by both stocks for 4, 5, 6, 7, 8, 9, and 10 rugae ornament the discs of 1, 9, 11, 3, 2, 0 and 0 pedicle valves of *L. salopiensis* compared with 0, 0, 0, 3, 5, 4 and 1 valves of *L. ventricosa*. Hence the larger disc of *L. salopiensis* bears significantly fewer rugae but this is understandable in that the average wavelength of the fifth ruga antero-medially of the umbo in 21 pedicle valves was 1.4 mm. (variance 0.058) whereas even the most distant rugae of *L. ventricosa* rarely attained a wavelength of 1 mm. Internally the two stocks are alike except for the less robust cardinal process, the less well developed notothyrial platform and the absence of striations on the teeth and sockets of *L. salopiensis* which differences are usually ascribed to excessive shell secretion and gerontism. The rhomboidal outline of the ventral muscle scar, for example is especially diagnostic for both species with an average percentage width relative to length of 89.0 (range 79–100) for 4 pedicle valves of *L. ventricosa* and of 85.0 (variance 290.5) for 13 valves of *L. salopiensis*. In summary then it may be said that despite many similarities, *L. salopiensis* is immediately distinguishable from *L. ventricosa* in its absolutely larger disc ornamented by fewer and coarser rugae.

The new species are most closely comparable with the type species of *Leptaena*, *L. rugosa* Dalman (see Spjeldnaes 1957 : 173) from the *Dalmanitina* beds and *L. veldrensis* Spjeldnaes (1957 : 179) from the *Coelosphaeridium* and *Mastopora* beds. From the former, however, both differ in the differently proportioned disc and the relatively longer and differently shaped ventral muscle scar and although they are like *L. veldrensis* in these features, the invariable presence of a rim to the ventral disc and the well defined pattern of rugation in both new species are reliable diagnostic differences.

### Genus **KIAEROMENA** Spjeldnaes 1957

TYPE SPECIES. *Leptaena kjerulfi* Høltedahl by original designation of Spjeldnaes (1957 : 72).

#### ***Kiaeromena cf. kjerulfi*** (Høltedahl)

(Pl. 16, figs. 1–5, 8)

DESCRIPTION. Concavo-convex, weakly geniculate and relatively elongate *Kiaeromena* with a poorly defined disc between 11 and 15 mm. long, over four-fifths as long as wide and with a ventral depth of about one-fifth the length and subtending a rounded angle of about 100° with the trail to give an overall depth of over two-fifths the length of the pedicle valve ; radial ornamentation unequally parvicostellate with 5 or 6 costellae per mm., at 10 mm. antero-medially of the ventral umbo ; 8 to 10 continuous, concentric asymmetrical rugae with wavelengths of about 1.5 mm. and steeper, shorter posterior sides also ornament the disc ; pseudo-deltidium and larger chilidium well developed, foramen small, rarely closed, supra-apical ; teeth small and widely splayed, continuous with short dental lamellae,



ventral muscle scar elongately oval, less than three-fifths as long as the disc and as wide as long in young valves but about four-fifths as wide as long in adult valves, adductor scars lanceolate, impressed anteriorly of a low median ridge and extending forwards for about three-fifths the length of the muscle field but not enclosed by the submedian lobes of the diductor scars ; cardinal process lobes long and slender, with a faint median ridge between them immediately below a slight indentation in the chilidium, notothyrial platform anchor-shaped with the lateral arms strengthening widely splayed socket ridges and together with the median ridge forming the posterior and median boundaries to a pair of subrounded dorsal adductor impressions that extend anteriorly for about one-third the length of the disc in young shells, slightly divergent submedian ridges within the dorsal adductor fields variably developed.

| MATERIAL (Figured).                                                           | length | width (mm.) |
|-------------------------------------------------------------------------------|--------|-------------|
| Internal mould of pedicle valve<br>(BB.29049)                                 | 21.0   | 23.0        |
| Incomplete internal and external<br>moulds of brachial valve<br>(BB.29050-51) | —      | —           |
| Fragment of external mould of<br>pedicle valve (BB.29052)                     | —      | —           |
| Internal mould of pedicle valve<br>(BB.29053)                                 | 14.0   | 17.0        |
| Internal mould of pedicle valve<br>(BB.29054)                                 | 20.0   | —           |

HORIZON AND LOCALITY. Allt Ddu Group : all specimens from fine sandstones and mudstones at the top of the Group and exposed in the north-west corner of the field 450 ft. south of Pand-y-isaf Farm.

DISCUSSION. The distinctive leptaenid *Kiaeromena* is fairly common in the highest Allt Ddu sandstones and siltstones although it is restricted to that horizon and the specimens are usually too deformed to permit more than a generic identification. Of all known species, however, the stock is closest to *K. kjerulfi* (Holtedahl) (see Spjeldnaes 1957 : 185) and, provisionally at least, must be regarded as conspecific with it. This is certainly true of ornamentation. Spjeldnaes emphasized the unequally parvicostellate nature of the Norwegian species and the prominence of the rugae, and the Bala specimens, with counts of 5 and 6 costellae per mm., 10 mm. antero-medially of the umbones of 2 and 3 pedicle valves respectively and with 8, 9 and 10 rugae ornamenting the discs of 3, 3 and 1 pedicle valves, are indistinguishable. The relative proportions of shell and muscle fields, too, are comparable. Indeed the only differences appear to be the relative smallness of the pseudodeltidium and the comparative simplicity of the cardinal process lobes of Bala shells, but both these features have been studied in only a few moulds and, in any event, such differences might have been nothing more than gerontic effects in the larger Norwegian shells.



Genus *BELLIMURINA* Cooper 1956

TYPE SPECIES. *Leptaena charlottae* Winchell & Schuchert by original designation of Cooper (1956 : 854).

*Bellimurina incommoda* sp. nov.

(Pl. 16, figs. 6, 7, 10-14)

DIAGNOSIS. Elongately semi-elliptical plano-convex *Bellimurina* with pedicle valve between three-fifths and two-thirds as long as wide and just over one-fifth as deep as long at umbo ; radial ornamentation strongly unequally parvicostellate, with counts of 7 or 8 costellae per mm., at 10 mm. anterior of ventral umbo, and interrupted by fine, closely spaced, concentric lamellae to give a microscopic reticulate pattern, entire surface also rugate with rugae vaguely disposed concentrically at intervals of about 0.5 mm. but impersistent and broken by stronger costae and costellae ; ventral interarea apsacline, apical foramen very small, pseudodeltidium small, dorsal interarea anacline, chilidium large and arched ; teeth large, tetrahedral, striated and ankylosed to widely divergent dental lamellae, ventral muscle field well defined over one-third as long as pedicle valve, and slightly longer than wide, rhomboidal in outline with elevated boundaries becoming indistinct anteriorly ; pedicle callist well developed passing into broad, raised median ridge becoming narrow and low anteriorly where it separates a pair of lanceolate adductor scars not enclosed by anterior ends of flanking diductor scars ; cardinal process lobes, squat and well developed, standing above anchor-shaped notothyrial platform that is extended and curved laterally to fuse with widely divergent socket ridges, and prolonged anteriorly as low median ridge reaching forwards for less than one-half the length of brachial valve and separating a pair of suboval adductor scars, each further divided by a low submedian ridge.

|            |                                                               | length | width (mm.) |
|------------|---------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Internal and external moulds of pedicle valve (BB.29055-56)   | 10.5   | 16.5        |
| PARATYPES. | Internal and external moulds of pedicle valve (BB.29057-58)   | —      | —           |
|            | Internal and external moulds of brachial valves (BB.29059-60) | —      | —           |
|            | Internal mould of brachial valve (BB.29061)                   | 12.0   | —           |

HORIZON AND LOCALITIES. Gelli-grŷn Group : BB.29055-56 from calcareous ash crags exposed 650 ft. south-east of Bryn-briglas Farm ; BB.29057-60 from calcareous ashes exposed below the Rhiwlas Limestone scarp on the north side of the northern outlier on Creigiau Bychain ; BB.29061 from calcareous ash crags just south of the track leading west from Gelli-grŷn Farm and 1,000 ft. west-south-west of the farm.



DISCUSSION. Rare strophomenaceid moulds represent the first record of *Bellimurina* in the Lower Palaeozoic rocks of South Britain. There is no doubt about the affinities of the stock ; the internal features as well as the highly distinctive ornamentation, show its close relationship to American and Scottish congeneric forms. But, in spite of the few specimens collected, the new species is immediately distinguishable, in its plane brachial valve and well-defined rhomboidal ventral muscle scar, from all other known ones which invariably have a gently convex brachial valve with a tendency to become geniculate in a ventral direction, and a significantly wider muscle scar. Other differences like the absence of a dorsal sulcus or a regularly zig-zag rugate pattern constitute additional contrasts with *B. sulcata* Cooper (1956 : 858) from the Pratt Ferry formations of Alabama or *B. concentrica* Cooper (1956 : 856) from the Pierce formation.

Very little information concerning the morphological variability of the new species can be added to that already given in the diagnosis except with regard to two features. Thus the unequally parvicostellate ornamentation is strongly developed—the costellae appear to be segregated into segments up to 0.5 mm. wide, and counts of 7 and 8 costellae per mm. were obtained for 1 and 2 pedicle valves 10 mm. antero-medially of the umbones. The rhomboidal ventral muscle scar is certainly less variable than one would expect because the average percentage length relative to the length of 6 internal moulds was 36.7 (variance 6.0) and the percentage width relative to length of 3 scars was 97, 94 and 84.

Superfamily RHYNCHONELLACEA Schuchert 1896

Family RHYNCHOTREMATIDAE Cooper 1956

Genus **ROSTRICELLULA** Ulrich & Cooper 1942

TYPE SPECIES. *Rostricellula rostrata* Ulrich & Cooper by original designation of Ulrich & Cooper (1942 : 625).

***Rostricellula sparsa* sp. nov.**

(Pl. 16, figs. 9, 15–17)

DIAGNOSIS. Broadly triangular in outline, almost four-fifths as long as wide with ventral apical angle of about 100°, unequally biconvex with brachial valve nearly two-fifths and pedicle valve about one-fifth as deep as wide, dorsal fold and ventral sulcus well defined, about two-fifths the maximum width of shell at strongly uniplicate anterior margin ; surface ornamented by narrowly angular costae with wavelength of 0.3–0.4 mm. on fold compared with 0.2 mm. on flanks at distance of 3 mm. from umbo ; two costae occupy the fold, with complementary median one in sulcus, and 4–6 finer ones occur on flanks ; dental lamellae fused with teeth, about one-seventh as long as pedicle valve, diverging at about 80° ; crural bases short, subtriangular in outline and not more than one-tenth as long as brachial valve, median ridge low but well defined represented externally by groove between submedian costae of dorsal fold.



|            |                                                                                          | length | width (mm.) |
|------------|------------------------------------------------------------------------------------------|--------|-------------|
| HOLOTYPE.  | Incomplete external and internal moulds of conjoined valves (BB.29039-40), dorsal aspect | 3.5    | 4.0 (est.)  |
| PARATYPES. | Incomplete external and internal moulds of brachial valve (BB.28893-94)                  | —      | 4.2         |
|            | Incomplete internal mould of brachial valve (BB.28892)                                   | 3.3    | —           |
|            | Internal mould of pedicle valve (BB.28977)                                               | 4.7    | 6.0         |

HORIZON AND LOCALITIES. Allt Ddu Group : BB.29039-40, BB.28893-94 from mudstone crags cropping out 1,100 yds. east of Pant-yr-onen Farm ; BB.28892, BB.28977 from mudstones just north of road and 320 yds. east-south-east of Glynbach.

DISCUSSION. Only five specimens of *Rostricellula* have been collected from the Caradoc rocks of the Bala district so that the quantitative estimates of various features given in the diagnosis, which never involve more than two specimens, are not important in the present systematic discrimination. The arrangement of the costae on the fold and in the sulcus is, however, highly distinctive. All American and the one known south British species of *Rostricellula* (*R. triangularis* Williams 1949 : 235) have at least two costae in the sulcus and three on the fold. Indeed only *R. ambigena* (Barrande) (see Havlíček 1961 : 51) from the Ashgillian of Czechoslovakia is comparable in the development of a costa in the sulcus and two costae on the fold. But these almost invariably bifurcate, or give rise by lateral branching to costellae, well within the size-range of the Bala specimens.

#### Superfamily SPIRIFERACEA Waagen 1893

##### Family CYCLOSPIRIDAE Schuchert 1913

##### Genus **CYCLOSPIRA** Hall & Clarke 1893

TYPE SPECIES. *Orthis bisulcata* Emmons by original designation of Hall & Clarke (1893 : 146).

#### *Cyclospira* sp.

(Pl. 16, fig. 18)

A few incomplete internal moulds of brachial valves belonging to the genus *Cyclospira* have been collected from the Gelli-grin Group and one (BB.28976), from calcareous ashes exposed in the quarry beside the drive to Y Garnedd Farm and 300 ft. south-east of the farm, is described and figured here to give some idea of the salient features. The mould is 3.0 mm. long and evidently represented an elongately oval, gently convex valve lacking ornamentation but indented posteriorly by a shallow median sulcus which passes anteriorly into a low fold. The divided



hinge-plate, which extended anteriorly for about one-tenth the length of the valve, was about twice as wide as long. It consisted of a pair of robust, triangular crural bases slightly raised along their postero-lateral edges to define a pair of oval sockets and continuous along their inner edges with slender, rod-like crura. The crural bases were undercut and unsupported; a thin, relatively high median septum originated just anterior of the hinge-line and extended anteriorly for about seven-tenths the length of the valve.

The valves are reminiscent of certain American *Cyclospira*, like *C. bisulcata* (Emmons) from the Trenton of New York State (see Cooper 1956 : 693), in the development of the fold anteriorly but until more is known of the species to which they belong, further comparison is unwarranted.

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# PLATE 1

## *Lingulella* cf. *ovata* (M'Coy)

Gelli-grin Group, calcareous ashes, 400 ft. east-south-east of Bryn-briglas Farm.

FIG. 1. Internal mould of pedicle valve. BB.28986.  $\times 1.3$ .

FIG. 2. Latex cast of external mould of pedicle valve. BB.28985.  $\times 1.3$ .

Calcareous ashy mudstones in old quarry 500 ft. west-south-west of Gelli-grin Farm.

FIG. 3. Internal mould of brachial valve. BB.28987.  $\times 3.6$ .

## *Pseudocrania* cf. *divaricata* M'Coy

Gelli-grin Group, calcareous ashes 500 ft. south-west of B.M.1338.7, Bryn Pig.

FIG. 4. Latex cast of dorsal exterior. BB.28988.  $\times 1$ .

FIG. 5. Internal mould of brachial valve. BB.28989.  $\times 2.1$ .

## *Paracraniops macella* gen. et sp. nov.

Gelli-grin Group, calcareous ashes in quarry near Y Garnedd Farm.

FIG. 6. Latex cast of ventral (?) exterior. BB.28991.  $\times 15$ .

FIG. 7. Holotype, internal mould of ventral (?) valve. BB.28990.  $\times 15$ .

FIG. 8. Internal mould of dorsal (?) valve. BB.28993.  $\times 10$ .

## *Orbiculoidea* sp.

Gelli-grin Group, calcareous ashes in old quarry, 500 ft. west of Gelli-grin Farm.

FIG. 9. Interior of brachial valve. BB.29135.  $\times 4.6$ .

## *Orthambonites cessata* sp. nov.

Gelli-grin Group, calcareous ashes at Myrddin Marad.

FIG. 10. Latex cast of ventral exterior. BB.29001.  $\times 3.8$ .

FIG. 14. Internal mould of pedicle valve. BB.29000.  $\times 3.8$ .

Calcareous ashes 400 ft. east-south-east of Bryn-briglas Farm.

FIG. 11. Internal mould of pedicle valve. BB.28998.  $\times 3.2$ .

FIG. 13. Latex cast of ventral exterior. BB.28999.  $\times 2.6$ .

Calcareous ashes 600 yds. north-east of Glyn-bach.

FIG. 12. Latex cast of dorsal interior. BB.28997.  $\times 5$ .

## *Nicolella actoniae* (J. de C. Sowerby)

Actonian Stage, in stream section by east side of road-bridge about 1,000 ft. west-south-west of Hatton.

FIG. 15. Latex cast of dorsal exterior. BB.27315.  $\times 1.7$ .

FIG. 19. Latex cast of dorsal interior. BB.27317.  $\times 1.5$ .

"Acton Scott", Shropshire.

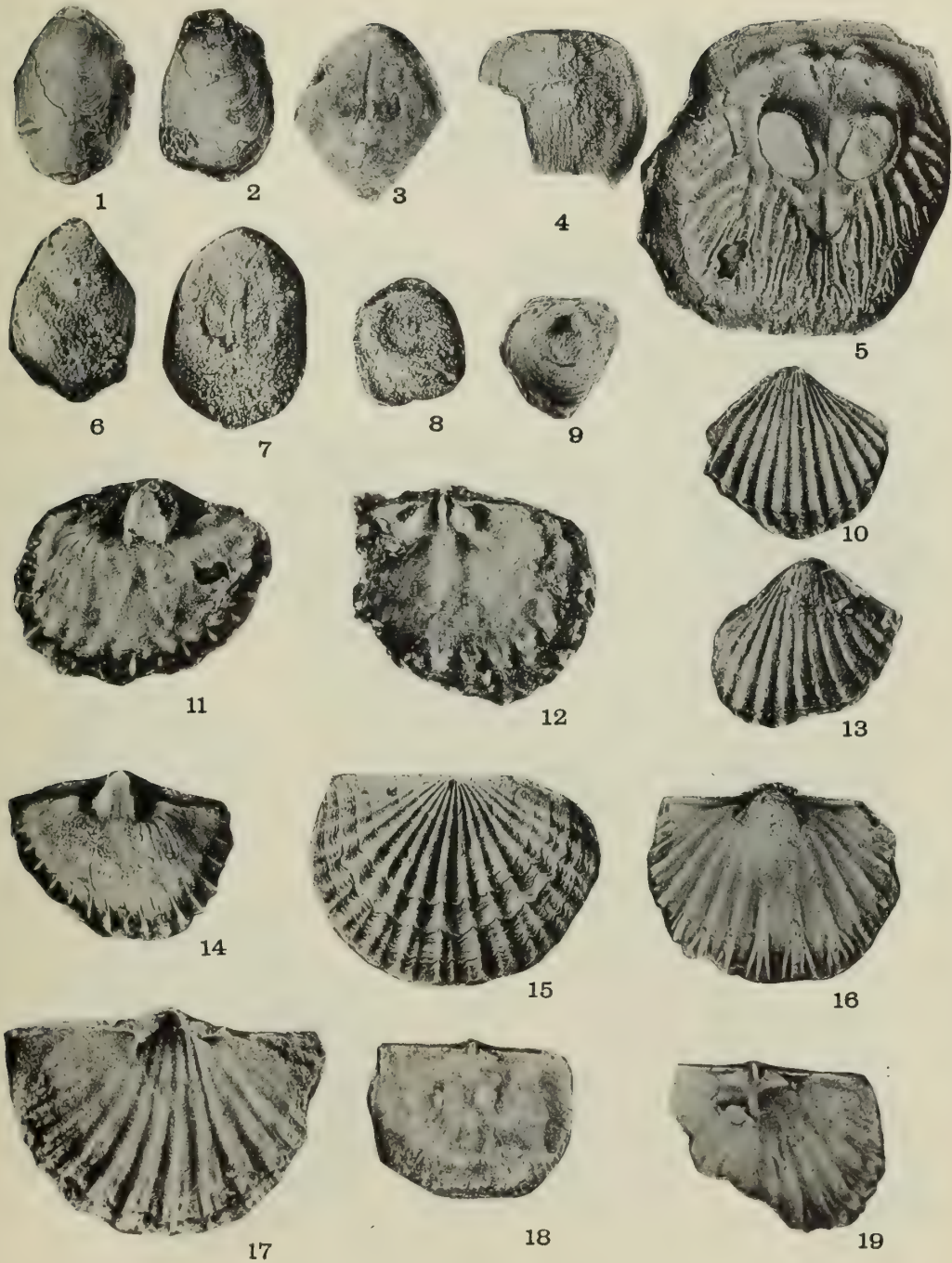
FIG. 16. Lectotype, internal mould of pedicle valve. G.S.M.6883.  $\times 1.5$ .

FIG. 17. Latex cast of ventral interior. B.74772.  $\times 1.8$ .

Loose blocks near Acton Scott Church.

FIG. 18. Latex cast of dorsal interior. BB.28959.  $\times 1.4$ .







## P L A T E 2

### *Nicolella actoniae obesa* subsp. nov.

Gelli-grin Group, calcareous ash in Ffridd Bach, south of Maes-meillion Farm.

FIG. 1. Latex cast of dorsal exterior. BB.29007.  $\times 2.2$ .

FIG. 2. Latex cast of dorsal exterior. BB.29005.  $\times 2.6$ .

FIG. 3. Latex cast of dorsal interior. BB.29006.  $\times 2.2$ .

Ashy mudstones exposed on the right bank of the Hirnant, 1,200 ft. east-north-east of Ty'n-y-wern Farm.

FIGS. 4, 5. Internal mould of pedicle valve, lateral and ventral views. BB.29004.  $\times 3.0$ .

Calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 7. Internal mould of pedicle valve. BB.29003.  $\times 2.2$ .

### *Dolerorthis duftonensis proluxa* subsp. nov.

Gelli-grin Group, calcareous ashes on Creigiau Bychain about 500 yds. north-east of Glynbach.

FIG. 6. Holotype, latex cast of dorsal exterior. BB.29009.  $\times 1.6$ .

FIG. 12. Holotype, internal mould of brachial valve. BB.29008.  $\times 1.4$ .

Ashy mudstones 1,600 ft. south-south-east of Bryn-bedwog Farm.

FIG. 8. Latex cast of ventral exterior. BB.29012.  $\times 1.6$ .

Calcareous ashes in old quarry, 1,100 ft. west-south-west of Gelli-grin Farm.

FIG. 9. Latex cast of dorsal interior. BB.29010.  $\times 2.2$ .

FIG. 13. Internal mould of pedicle valve. BB.29014.  $\times 1.1$ .

Calcareous ashes in quarries 650 ft. west-north-west of BM.1407.6, Bryn Pig.

FIG. 10. Latex cast of dorsal exterior. BB.29013.  $\times 1.6$ .

FIG. 11. Internal mould of pedicle valve. BB.29011.  $\times 1.8$ .

### *Dolerorthis* sp.

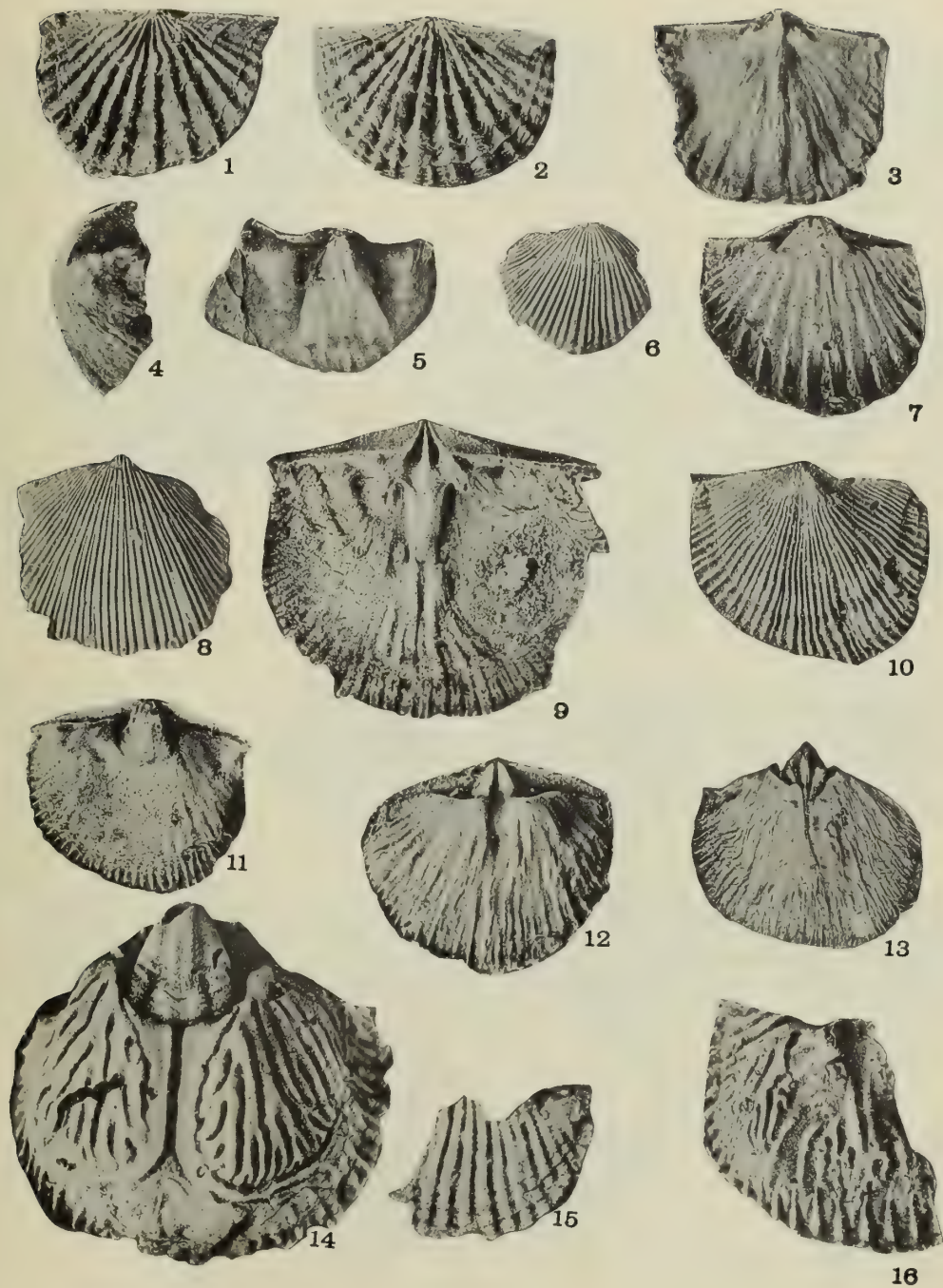
Allt Ddu Group, siltstones about 80 ft. north of the gutter on Craig y Gath.

FIG. 14. Internal mould of pedicle valve. BB. 29152.  $\times 4.6$ .

FIG. 15. Latex cast of fragment of dorsal (?) exterior. BB.29154.  $\times 4.0$ .

FIG. 16. Incomplete internal mould of brachial valve. BB.29153.  $\times 4.9$ .







## PLATE 3

### *Dinorthis flabellulum* (J. de C. Sowerby)

Costonian Stage, sandstones at Coston Farm, one mile east-south-east of Clunbury.

FIG. 1. Latex cast of ventral exterior. BB.28935.  $\times 1.9$ .

FIG. 2. Latex cast of dorsal interior. BB.29023.  $\times 1.3$ .

FIG. 3. Latex cast of dorsal exterior. BB.29024.  $\times 1.3$ .

FIG. 4. Internal mould of pedicle valve. BB.28934.  $\times 1.3$ .

### *Dinorthis berwynensis* (Whittington)

Glyn Gower Group, siltstones 1,300 ft. south-south-east of Coed-y-foel-uchaf Farm.

FIG. 6. Internal mould of pedicle valve. BB.28982.  $\times 4.3$ .

Siltstone crags in wood immediately east of Cefn-bodig Farm.

FIG. 9. Internal mould of brachial valve. BB.28983.  $\times 1.7$ .

FIG. 10. Latex cast of ventral exterior. BB. 28984.  $\times 1.7$ .

Allt Ddu Group, siltstones 600 ft. north of Frondderw Farm.

FIG. 5. Internal mould of brachial valve. BB.29025.  $\times 6.6$ .

### *Dinorthis berwynensis angusta* subsp. nov.

Allt Ddu Group, fine sandstones immediately below the Pont-y-Ceunant Ash north of Y Garnedd Farm.

FIG. 7. Holotype, latex cast of ventral exterior. BB.28979.  $\times 1.4$ .

FIG. 8. Holotype, internal mould of pedicle valve. BB.28978.  $\times 1.4$ .

FIG. 11. Latex cast of ventral exterior. BB.28981.  $\times 1.7$ .

FIG. 12. Internal mould of pedicle valve. BB.28980.  $\times 2.2$ .

FIG. 13. Internal mould of brachial valve. BB.29027.  $\times 2.1$ .

FIG. 14. Internal mould of brachial valve. BB.29026.  $\times 2.2$ .

### *Platystrophia* cf. *sublimis* (Öpik)

Gelli-grin Group, calcareous ashes 500 ft. south-west of BM.1338.7, Bryn Pig.

FIG. 15. Latex cast of ventral exterior. BB.29019.  $\times 1.7$ .

FIG. 16. Latex cast of dorsal exterior. BB.29022.  $\times 3.1$ .

FIG. 17. Internal mould of brachial valve. BB.29021.  $\times 3.7$ .

FIG. 19. Latex cast of ventral exterior. BB.29020.  $\times 1.4$ .

FIG. 20. Internal mould of pedicle valve. BB.29016.  $\times 1.1$ .

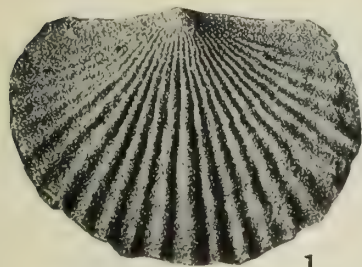
FIG. 21. Latex cast of dorsal interior. BB.29015.  $\times 1.5$ .

FIG. 22. Latex cast of dorsal exterior. BB.29017.  $\times 1.7$ .

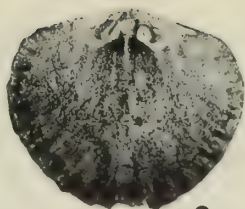
Calcareous ashes on the south side of the head of the stream issuing from Craig y Gath.

FIG. 18. Latex cast of ventral exterior. BB.29018.  $\times 1.5$ .

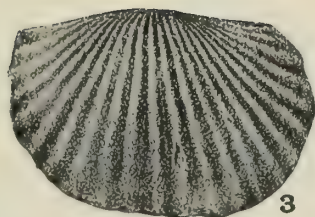




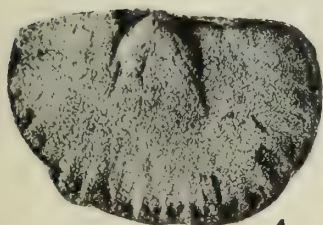
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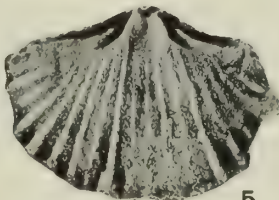
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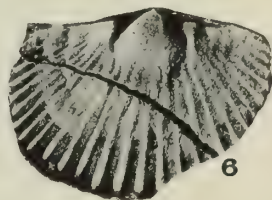
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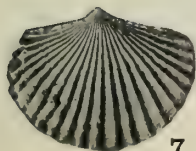
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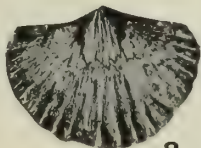
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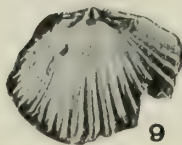
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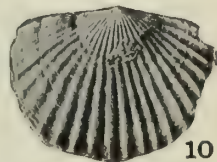
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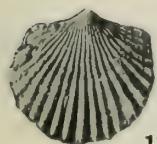
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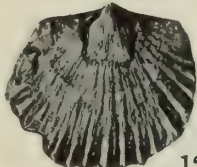
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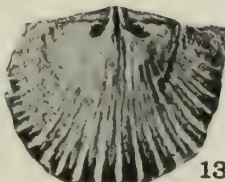
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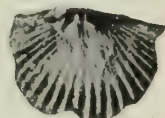
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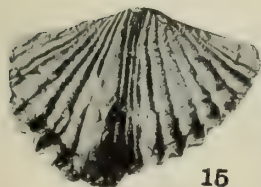
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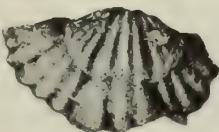
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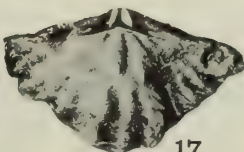
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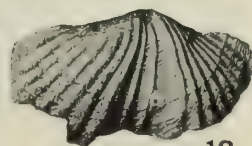
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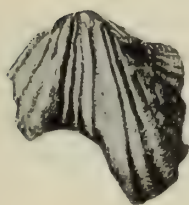
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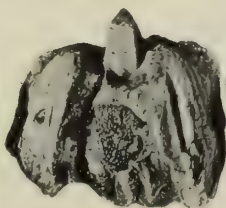
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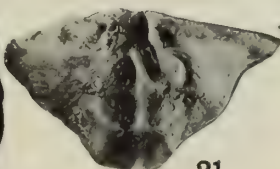
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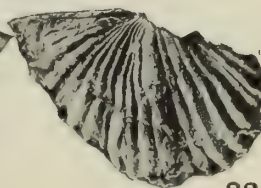
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# PLATE 4

## *Rhactorthis crassa* gen. et sp. nov.

Calcareous ashes on Creigiau Bychain.

FIG. 1. Internal mould of pedicle valve. BB.28883.  $\times 3.3$ .

Calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 2. Holotype, internal mould of brachial valve. BB.28878.  $\times 6.6$ .

FIG. 4. Internal mould of pedicle valve. BB.24542.  $\times 3.5$ .

Gelli-grin Group, calcareous ashes on Creigiau Bychain.

FIG. 3. Internal mould of brachial valve BB.29028.  $\times 2.8$ .

FIG. 6. Latex cast of dorsal exterior. BB.28879  $\times 3.2$ .

Calcareous ashes 600 ft. south-east of Bryn-briglas.

FIG. 5. Latex cast of ventral exterior. BB.28881.  $\times 3.1$ .

## *Skenidioides* cf. *costatus* Cooper

Gelli-grin Group, calcareous ashes on Creigiau Bychain.

FIG. 7. Latex cast of ventral interior. BB.28918.  $\times 5.8$ .

FIG. 8. Internal mould of pedicle valve. BB.28924.  $\times 5.6$ .

FIG. 9. Latex cast of ventral interior. BB.28921.  $\times 5.5$ .

FIG. 10. Internal mould of brachial valve. BB.28917.  $\times 6.4$ .

FIG. 11. Internal mould of brachial valve. BB.28919.  $\times 4.7$ .

FIG. 13. Latex cast of ventral exterior. BB.28922.  $\times 7.4$ .

FIG. 14. Latex cast of dorsal exterior. BB.28920.  $\times 6.2$ .

Calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 12. Internal mould of brachial valve. BB.24548.  $\times 3.3$ .

## *Cremnorthis parva* gen. et sp. nov.

Gelli-grin Group, calcareous ashes in old quarry 1,100 ft. west-south-west of Gelli-grin Farm.

FIG. 15. Internal mould of pedicle valve. BB.28897.  $\times 6.4$ .

FIG. 16. Latex cast of ventral interior. BB.28897.  $\times 6.4$ .

FIG. 17. Internal mould of brachial valve. BB.28896.  $\times 7.0$ .

FIG. 18. Latex cast of dorsal exterior. BB.28898.  $\times 6.1$ .

FIGS. 19, 20. Latex cast of exterior of conjoined valves, lateral and dorsal aspects. BB.28900.  $\times 6.1$ .

FIG. 21. Latex cast of ventral exterior. BB.28899.  $\times 14.2$ .

FIG. 22. Holotype, internal mould of brachial valve. BB.28923.  $\times 8.5$ .

FIG. 23. Holotype, latex cast of dorsal interior. BB.28923.  $\times 9.6$ .

## *Dalmanella modica* sp. nov.

Gelli-grin Group, calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 24. Latex cast of dorsal exterior. BB.24603.  $\times 3.5$ .

Calcareous ashes 1,000 ft. west-south-west of Gelli-grin Farm.

FIG. 25. Internal mould of brachial valve. BB.29131.  $\times 2.6$ .



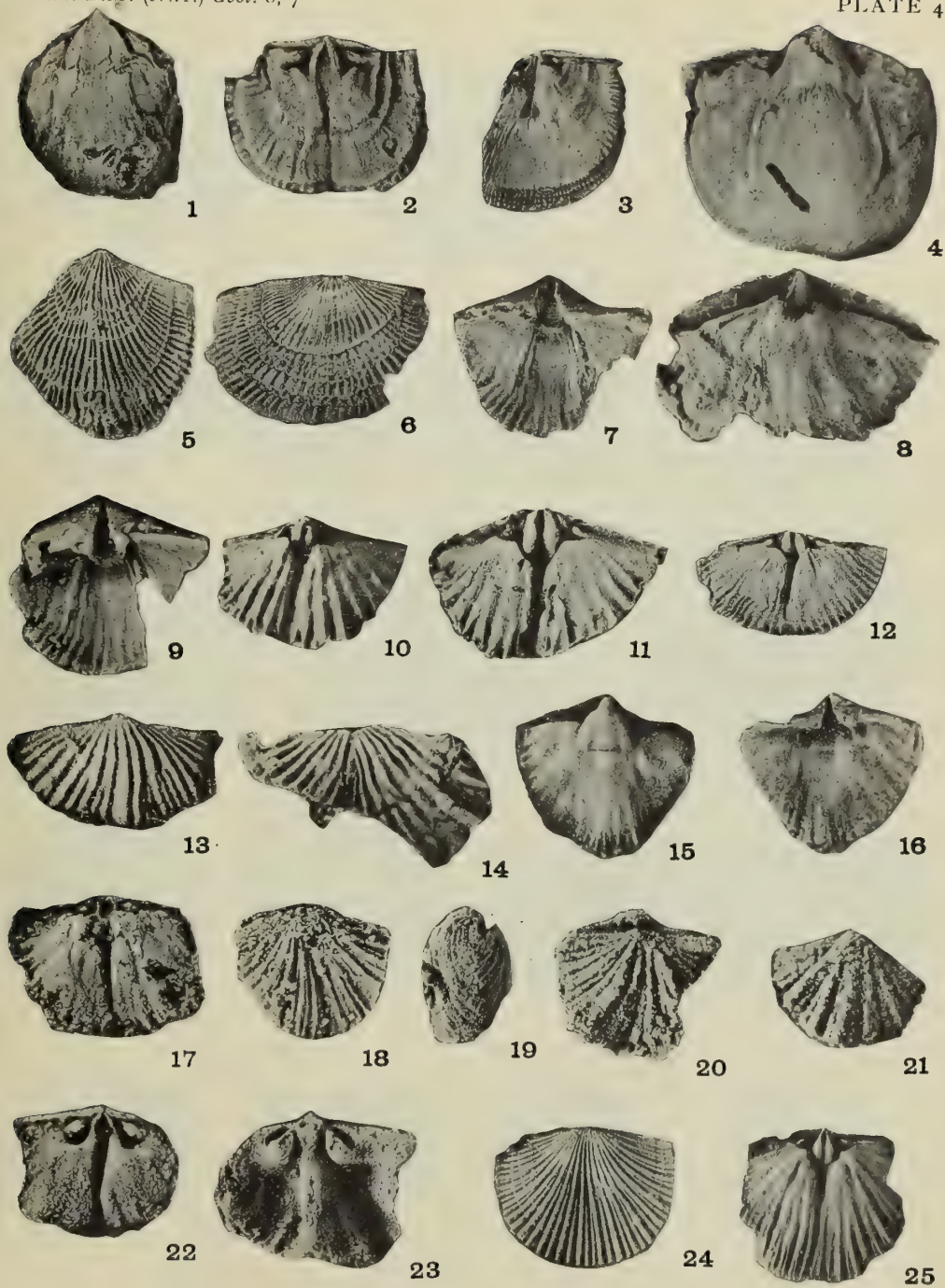




PLATE 5

*Dalmanella modica* sp. nov.

Gelli-grin Group, calcareous ashes 1,000 ft. west-south-west of Gelli-grin Farm.

FIG. 1. Internal mould of brachial valve. BB.29029.  $\times 3.6$ .

FIG. 4. Latex cast of ventral exterior. BB.28963.  $\times 2.6$ .

FIG. 6. Internal mould of pedicle valve. BB.28964.  $\times 2.6$ .

Calcareous ashes 700 ft. west-north-west of BM.1338.7, Bryn Pig.

FIG. 2. Latex cast of dorsal exterior. BB.28966.  $\times 2.7$ .

FIG. 7. Latex cast of dorsal exterior. BB.28967.  $\times 2.4$ .

Calcareous ashes in Ffridd Bach, south of Maes-meillion.

FIG. 3. Holotype, dorsal aspect of internal mould of conjoined valves. BB.28960.  $\times 2.7$ .

Calcareous ashes, Creigiau Bychain.

FIG. 5. Internal mould of pedicle valve. BB.28962.  $\times 4.1$ .

*Howellites striata* Bancroft

Allt Ddu Group, siltstones in gutter section on Craig y Gath, 3,400 ft. south of Glyn Mawr.

FIG. 8. Latex cast of dorsal interior. BB.24650.  $\times 3.1$ .

FIG. 12. Latex cast of dorsal exterior. BB.24650.  $\times 3.1$ .

FIG. 13. Latex cast of ventral exterior. BB.24651.  $\times 3.3$ .

FIG. 17. Internal mould of pedicle valve. BB.24652.  $\times 2.1$ .

Siltstone crags on Craig y Gath, 880 ft. east of Ty'n-y-cefn Farm.

FIG. 9. Latex cast of dorsal interior. BB.28926.  $\times 4.1$ .

FIG. 11. Latex cast of dorsal exterior. BB.28927.  $\times 2.6$ .

FIG. 14. Internal mould of pedicle valve. BB.28925.  $\times 2.9$ .

Siltstone crags on Craig y Gath, 1,000 ft. east of Ty'n-y-cefn Farm.

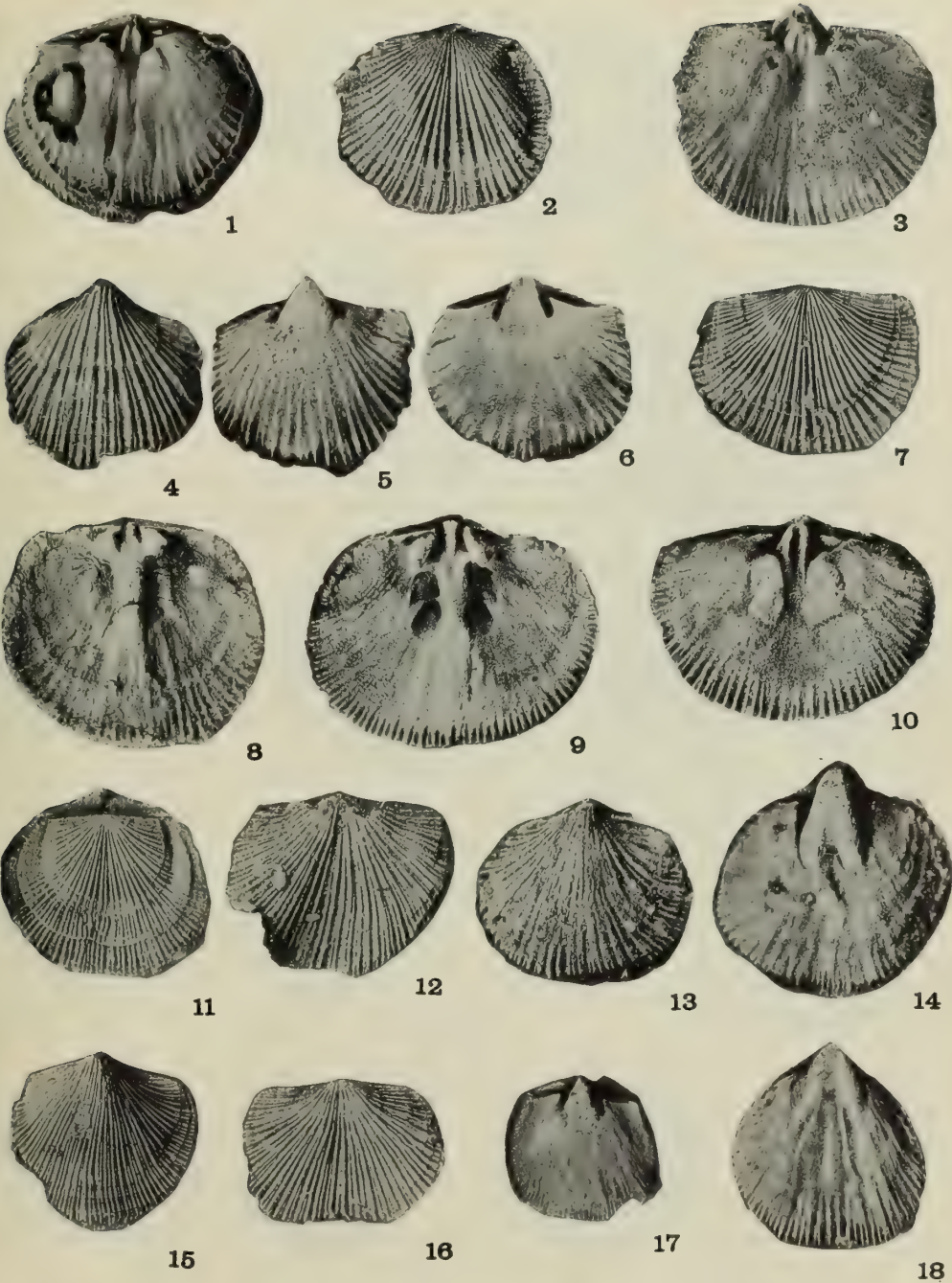
FIG. 10. Internal mould of brachial valve. BB.28928.  $\times 3.6$ .

FIG. 15. Latex cast of ventral exterior. BB.28931.  $\times 2.4$ .

FIG. 16. Latex cast of dorsal exterior. BB.28930.  $\times 3.8$ .

FIG. 18. Internal mould of pedicle valve. BB.28929.  $\times 3.4$ .







## PLATE 6

### *Howellites intermedia* Bancroft

Allt Ddu Group, siltstone crags on Craig y Gath, 120 yds. east of ford, 2,200 ft. south of Ty'n-y-cefn Farm.

- FIG. 1. Internal mould of brachial valve. BB.28936.  $\times 3$ .
- FIG. 2. Latex cast of dorsal exterior. BB.28939.  $\times 2.3$ .
- FIG. 3. Latex cast of dorsal exterior. BB.28938.  $\times 3.7$ .
- FIG. 4. Internal mould of pedicle valve. BB.28937.  $\times 3$ .
- FIG. 5. Latex cast of ventral exterior. BB.28940.  $\times 2.8$ .

### *Howellites ultima* Bancroft

Allt Ddu Group, siltstones 80 ft. north of the gutter on Craig y Gath.

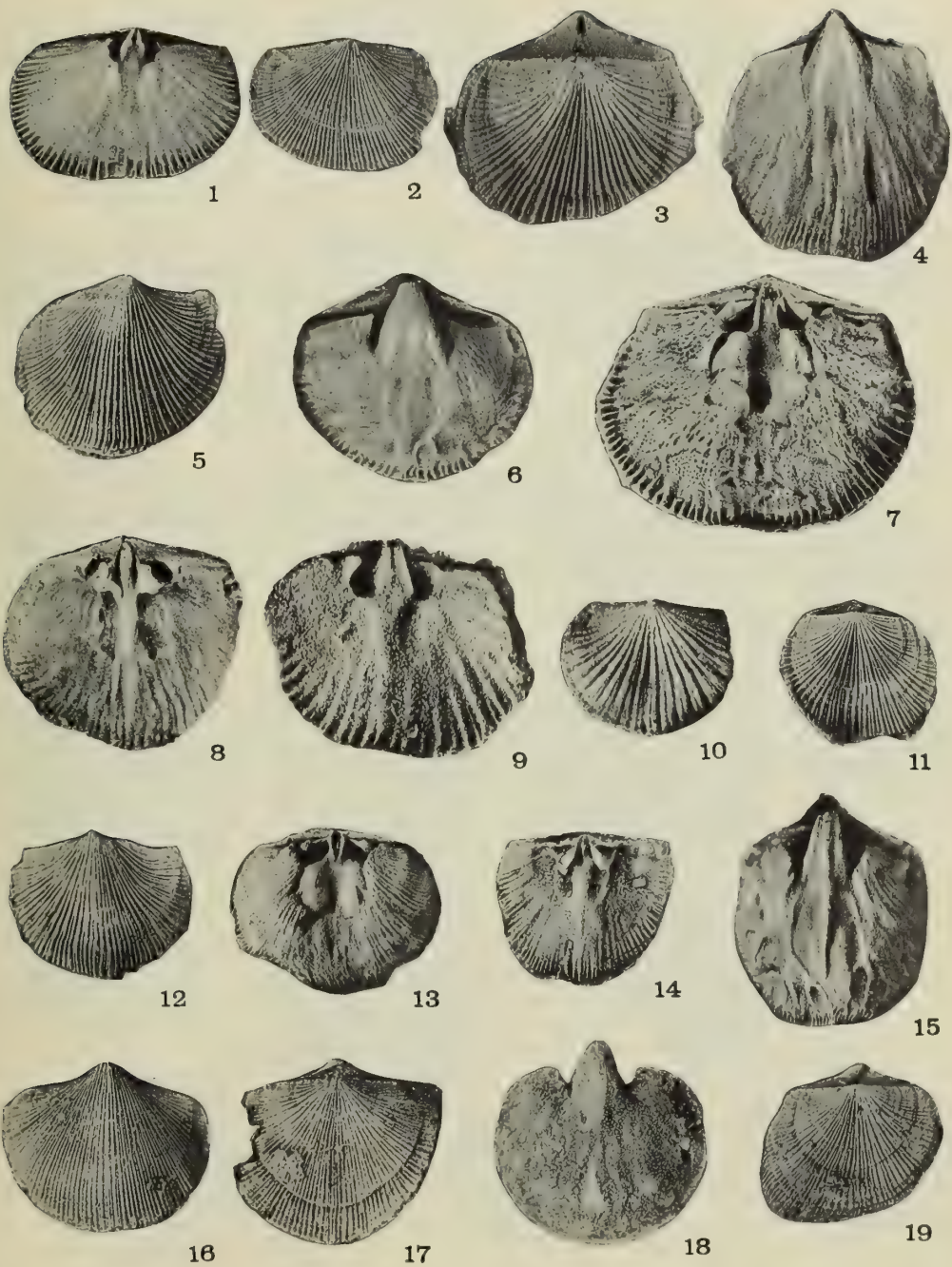
- FIG. 6. Internal mould of pedicle valve. BB.28941.  $\times 3.2$ .
- FIG. 7. Internal mould of brachial valve. BB.28944.  $\times 3.8$ .
- FIG. 8. Latex cast of dorsal interior. BB.28943.  $\times 2.2$ .
- FIG. 9. Internal mould of brachial valve. BB.28942.  $\times 6.6$ .
- FIG. 10. Latex cast of dorsal exterior. BB.28945.  $\times 4.8$ .
- FIG. 11. Latex cast of dorsal exterior. BB.28946.  $\times 2.3$ .
- FIG. 12. Latex cast of ventral exterior. BB.28947.  $\times 2.5$ .

### *Howellites antiquior* (M'Coy)

Gelli-grŷn Group, calcareous ashes 700 ft. west-north-west of BM.1338.7, Bryn Pig.

- FIG. 13. Internal mould of brachial valve. BB.28950.  $\times 2.8$ .
- FIG. 19. Latex cast of dorsal exterior. BB.28952.  $\times 2.3$ .
- Calcareous ashes in old quarries in Ffridd Bach, south of Maes-meillion.
- FIG. 14. Latex cast of dorsal interior. BB.28951.  $\times 3.3$ .
- FIG. 15. Internal mould of pedicle valve. BB.28949.  $\times 3.5$ .
- FIG. 17. Latex cast of dorsal exterior. BB.28953.  $\times 2.6$ .
- FIG. 18. Ventral aspect of internal mould of conjoined valves. BB.28948.  $\times 3.2$ .
- Calcareous ashes in Ffridd Bach, south of Maes-meillion.
- FIG. 16. Latex cast of ventral exterior. BB.25043.  $\times 2.3$ .







## PLATE 7

### *Howellites antiquior* (M'Coy)

Lower Longvillian Substage, siltstones on Gallt-yr-ancr, 440 yds. north of west of Dyffryn.

FIG. 1. Latex cast of ventral exterior. BB.28957.  $\times 3.2$ .

FIG. 2. Internal mould of pedicle valve. BB.28956.  $\times 3$ .

FIG. 5. Latex cast of dorsal exterior. BB.28958.  $\times 3.2$ .

FIG. 6. Latex cast of dorsal interior. BB.28955.  $\times 2.9$ .

### *Onniella ostentata* sp. nov.

Gelli-grin Group, calcareous ashes 850 ft. west of Gelli-grin Farm.

FIG. 3. Internal mould of brachial valve. BB.28868.  $\times 3.3$ .

FIG. 8. Latex cast of dorsal exterior. BB. 28869.  $\times 2.4$ .

Calcareous ashes 1,900 ft. east-north-east of Bryn-briglas Farm.

FIG. 4. Latex cast of dorsal exterior. BB.28867.  $\times 2.3$ .

Calcareous ashes in Ffridd Bach, south of Maes-meillion.

FIG. 7. Holotype, internal mould of brachial valve. BB.29030.  $\times 3.4$ .

FIG. 11. Internal mould of pedicle valve. BB.28870.  $\times 3.5$ .

FIG. 16. Latex cast of ventral exterior. BB.28871.  $\times 2.8$ .

Calcareous ashes on Creigiau Bychain.

FIG. 9. Latex cast of dorsal interior. BB.28866.  $\times 5.1$ .

FIG. 10. Latex cast of dorsal interior. BB.28933.  $\times 3$ .

### *Onniella* cf. *soudleyensis* (Bancroft)

Nant Hir Group, mudstones on left bank of Nant Hir, 600 ft. north-east of Cefn-y-maes Farm.

FIG. 12. Latex cast of dorsal interior. BB.28874.  $\times 2.6$ .

FIG. 13. Latex cast of ventral exterior. BB.28875.  $\times 2.5$ .

FIG. 14. Latex cast of dorsal exterior. BB.28876.  $\times 2.8$ .

FIG. 15. Internal mould of pedicle valve. BB.28872.  $\times 3.3$ .

FIG. 17. Latex cast of dorsal exterior. BB.28877.  $\times 5.1$ .

FIG. 18. Internal mould of brachial valve. BB.28873.  $\times 5.5$ .

### *Bancroftina* sp.

Gelli-grin Group, calcareous ashes in old quarries 1,800 ft. south of Bryn-melyn Farm.

FIG. 19. Ventral aspect of internal mould of conjoined valves. BB.29147.  $\times 2$ .

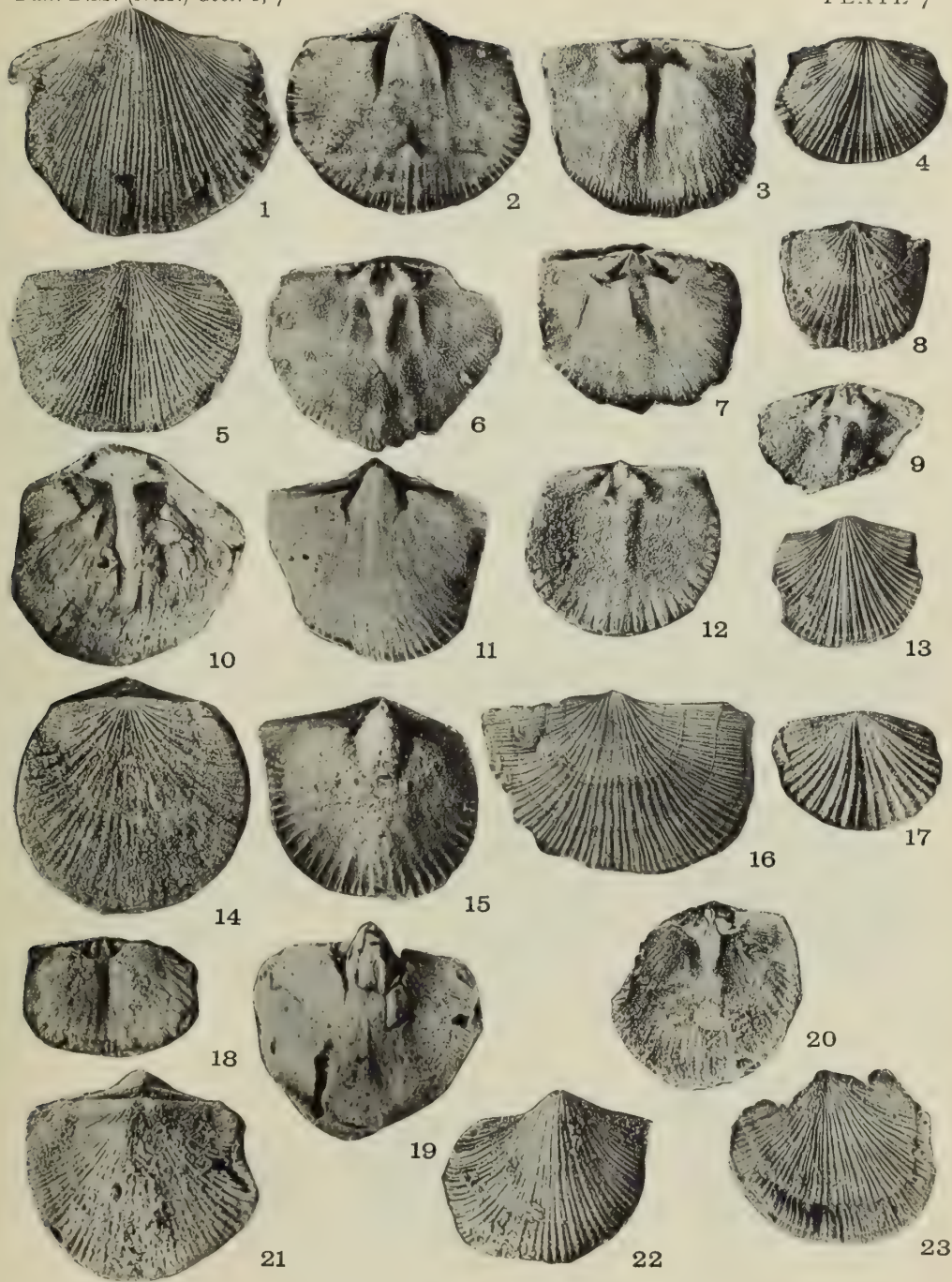
FIG. 20. Latex cast of dorsal interior. BB.29149.  $\times 1.6$ .

FIG. 21. Latex cast of dorsal exterior. BB.29146.  $\times 2$ .

FIG. 22. Latex cast of ventral exterior. BB.29124.  $\times 2$ .

FIG. 23. Latex cast of dorsal exterior. BB.29148.  $\times 1.4$ .







# PLATE 8

## *Reuschella* cf. *horderleyensis* Bancroft

Allt Ddu Group, mudstones 1,200 ft. west-north-west of Rhiwlas House.

- FIGS. 1, 2. Ventral and dorsal aspects of internal mould of conjoined valves. BB.29132.  $\times 1.5$ .  
 FIG. 3. Latex cast of dorsal interior. BB.28974.  $\times 1.9$ .  
 FIG. 4. Internal mould of brachial valve. BB.28971.  $\times 1.6$ .  
 FIG. 5. Internal mould of pedicle valve. BB.28973.  $\times 1.6$ .  
 FIG. 6. Latex cast of dorsal exterior. BB.28972.  $\times 1.9$ .  
 FIG. 7. Internal mould of brachial valve. BB.28968.  $\times 2.9$ .  
 FIG. 8. Latex cast of dorsal exterior. BB.28969.  $\times 2.9$ .  
 FIG. 9. Latex cast of ventral exterior. BB.28975.  $\times 1.3$ .  
 FIG. 10. Internal mould of pedicle valve. BB.28970.  $\times 4.3$ .

## *Reuschella horderleyensis undulata* subsp. nov.

Gelli-grin Group, calcareous ashes in quarries 650 ft. west-north-west of BM.1407.6, Bryn Pig.

- FIG. 11. Latex cast of ventral exterior. BB.28863.  $\times 1.4$ .  
 Calcareous ashes 500 ft. south-west of BM.1338.7, Bryn Pig.  
 FIG. 12. Latex cast of ventral exterior. BB.29031.  $\times 1.5$ .  
 Calcareous ashes 1,900 ft. north-east of Bryn-briglas Farm.  
 FIG. 13. Holotype, internal mould of pedicle valve. BB.28860.  $\times 1.6$ .  
 Calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.  
 FIG. 14. Latex cast of dorsal interior. BB.28865.  $\times 1.7$ .  
 FIG. 15. Latex cast of dorsal exterior. BB.28861.  $\times 2$ .  
 FIG. 16. Internal mould of brachial valve. BB.28862.  $\times 1.7$ .  
 Ashy mudstones 1,200 ft. east-north-east of Ty'n-y-wern Farm.  
 FIG. 17. Internal mould of brachial valve. BB.28864.  $\times 3.9$ .



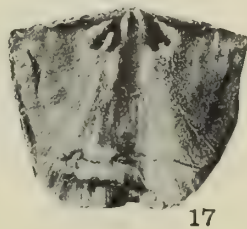
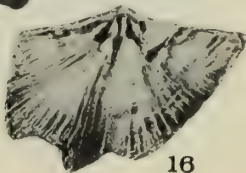
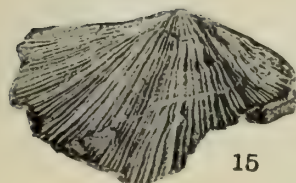
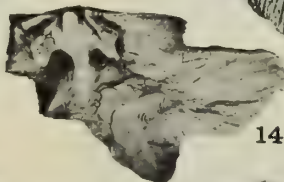
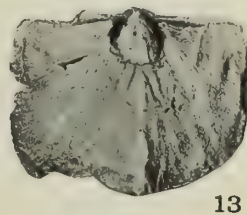
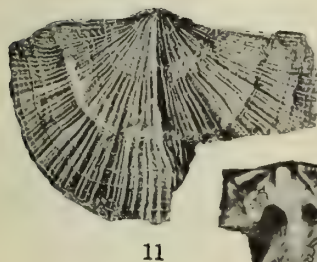
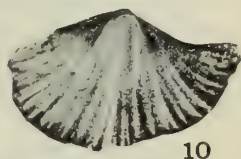
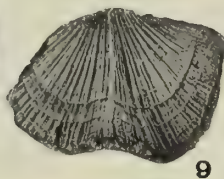
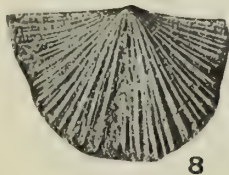
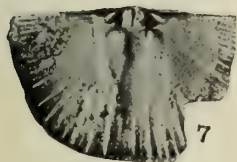
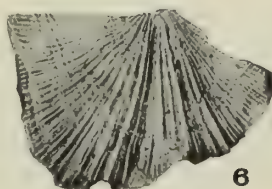
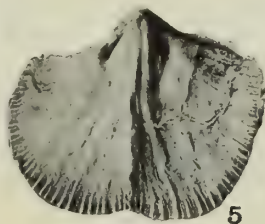
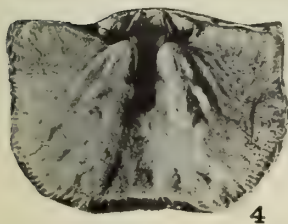
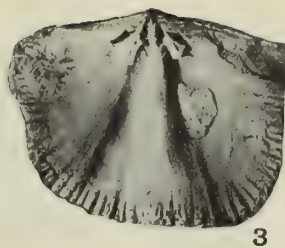
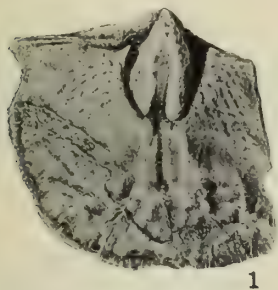




PLATE 9

*Heterorthis alternata* (J. de C. Sowerby)

Upper Longvillian Substage, Alternata Limestone in Soudley quarry, 2 miles south-east of Church Stretton.

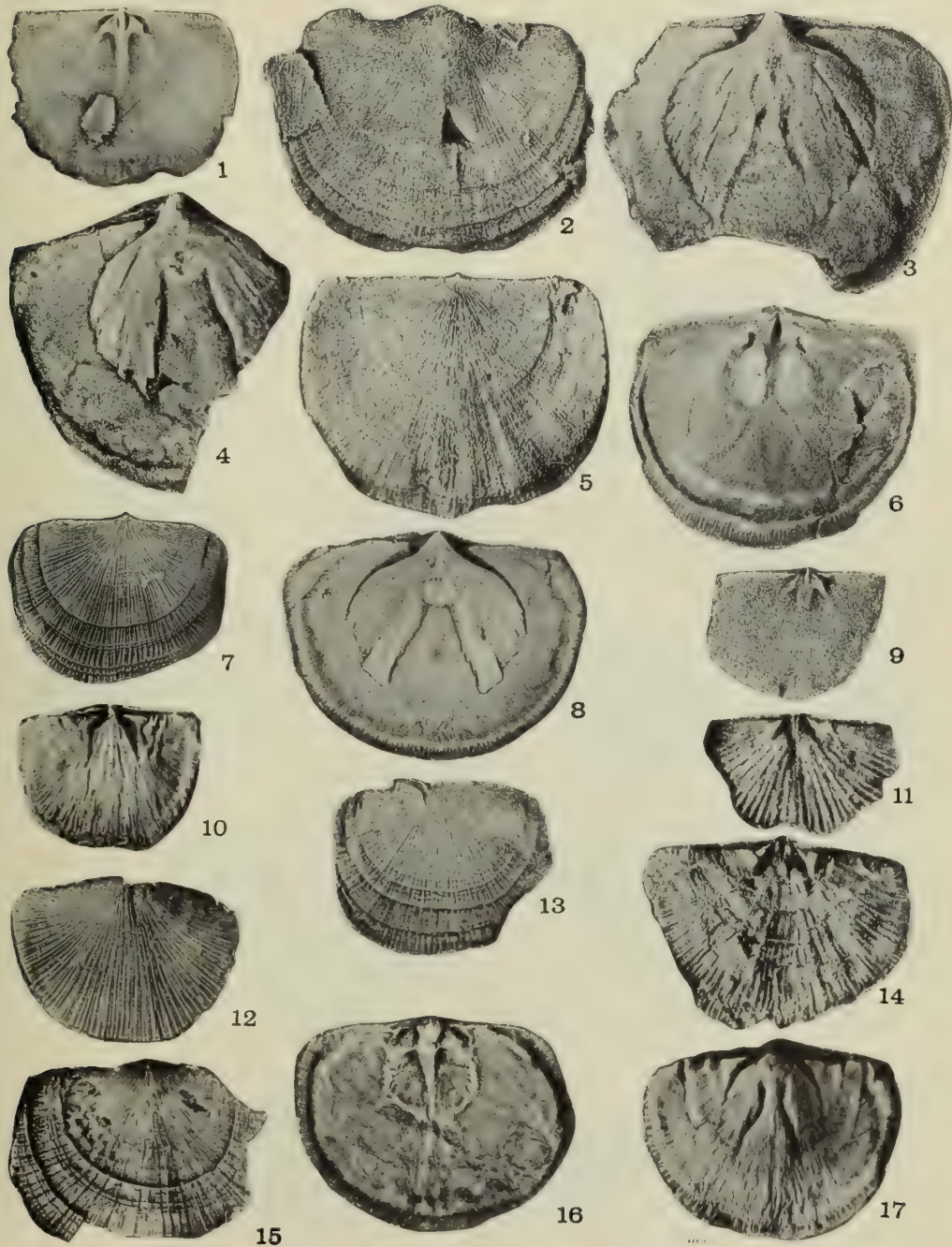
- FIG. 1. Latex cast of dorsal interior. BB.28904.  $\times 1.4$ .  
FIG. 2. Latex cast of ventral exterior. BB.29134.  $\times 1.7$ .  
FIG. 3. Internal mould of pedicle valve. BB.28901.  $\times 1.8$ .  
FIG. 4. Internal mould of pedicle valve. BB.28907.  $\times 1.8$ .  
FIG. 5. Latex cast of dorsal exterior. BB. 28903.  $\times 1.5$ .  
FIG. 6. Internal mould of brachial valve. BB.28906.  $\times 1.5$ .  
FIG. 8. Internal mould of pedicle valve. BB.28905.  $\times 1.5$ .  
FIG. 9. Latex cast of dorsal interior. BB.28902.  $\times 2.7$ .

*Heterorthis* cf. *retrorsistria* (M'Coy)

Allt. Ddu Group, mudstones 1,200 ft. west-north-west of Rhiwlas House.

- FIG. 7. Latex cast of dorsal exterior. BB.28913.  $\times 1.6$ .  
FIG. 10. Internal mould of pedicle valve. BB.28910.  $\times 2.8$ .  
FIG. 11. Internal mould of brachial valve. BB.28954.  $\times 5.7$ .  
FIG. 12. Latex cast of ventral exterior. BB.28912.  $\times 2$ .  
FIG. 13. Latex cast of dorsal exterior. BB.28913.  $\times 1.6$ .  
FIG. 14. Internal mould of brachial valve. BB.28916.  $\times 3.6$ .  
FIG. 15. External mould of brachial valve. BB.28911.  $\times 1.5$ .  
FIG. 16. Latex cast of dorsal interior. BB.28908.  $\times 2$ .  
FIG. 17. Internal mould of pedicle valve. BB.28914.  $\times 2.1$ .







# PLATE 10

## *Salopia* sp.

Gelli-grŷn Group, calcareous ashes 850 ft. west of Gelli-grŷn Farm.

FIGS. 1, 2. Latex cast and mould of dorsal interior. BB.28915.  $\times 4.5$ .

## *Bicuspina spiriferoides* (M'Coy)

Gelli-grŷn Group, "Limestone schists of Bala".

FIG. 3. Internal mould of pedicle valve. A.42458.  $\times 3.2$ .

FIGS. 5, 9. Lectotype, latex cast and mould of dorsal interior. A.42457a.  $\times 1.7$ .

FIG. 6. Lectotype, latex cast of dorsal exterior. A.42457b.  $\times 3.7$ .

FIG. 7. Lectotype, latex cast of ventral exterior. A.42457c.  $\times 1.8$ .

Calcareous ashes 300 ft. south of Y Garnedd Farm.

FIG. 4. Internal mould of pedicle valve. BB.29034.  $\times 1.4$ .

Calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 8. Latex cast of ventral exterior. BB.29033.  $\times 1.6$ .

Calcareous ashes 1,100 ft. west of Gelli-grŷn Farm.

FIG. 10. Latex cast of dorsal exterior. BB.29032.  $\times 2.1$ .

## *Oxoplectia* sp.

Gelli-grŷn Group, calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 11. Latex cast of dorsal exterior. BB.29037.  $\times 1.8$ .

FIG. 12. Latex cast of ventral exterior. BB.29035.  $\times 2.8$ .

FIG. 13. Latex cast of dorsal interior. BB.29038.  $\times 2.1$ .

FIG. 17. Internal mould of pedicle valve. BB.24622.  $\times 2.8$ .

## *Vellamo* sp.

Allt Ddu Group, siltstones 1,950 ft. east of Llaithgwm Farm.

FIG. 14. Latex cast of ventral exterior. BB.28965.  $\times 1.2$ .

FIG. 18. Internal mould of pedicle valve. BB.29133.  $\times 1.2$ .

## *Leptestiina oepiki* (Whittington)

Gelli-grŷn Group, calcareous ashes on Creigiau Bychain.

FIG. 15. Internal mould of pedicle valve. BB.28886.  $\times 4.7$ .

Calcareous ashes in old quarries in Ffridd Bach, south of Maes-meillion Farm.

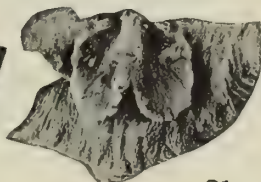
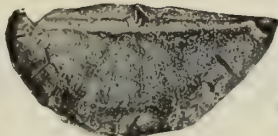
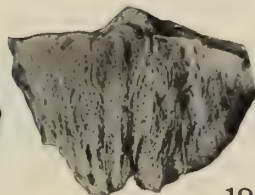
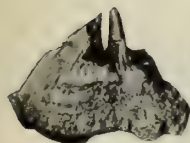
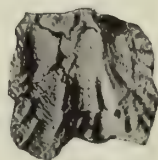
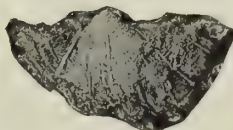
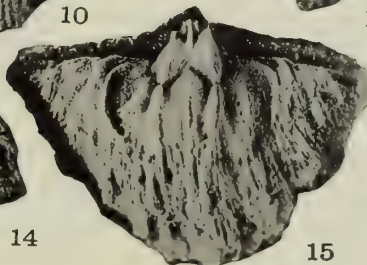
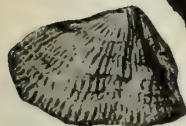
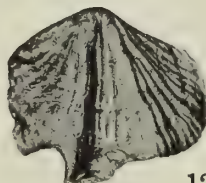
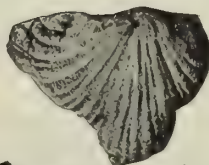
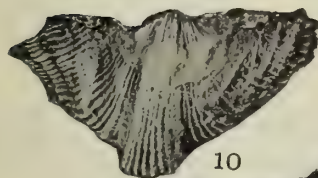
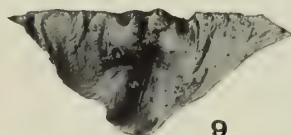
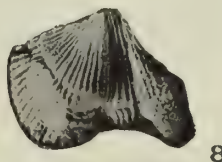
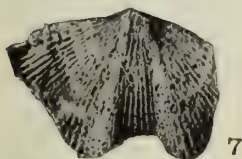
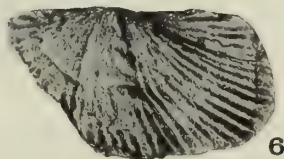
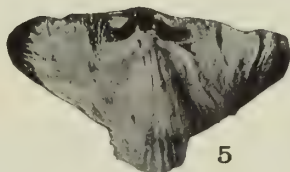
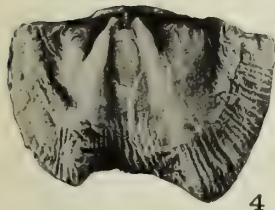
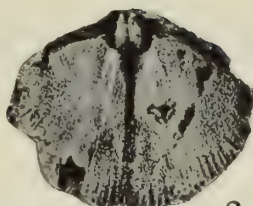
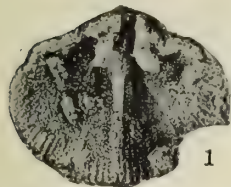
FIG. 16. Latex cast of ventral exterior. BB.28888.  $\times 2.7$ .

FIG. 19. Internal mould of pedicle valve. BB.28890.  $\times 3.8$ .

FIG. 20. Latex cast of dorsal exterior. BB.28889.  $\times 3.6$ .

FIG. 21. Latex cast of dorsal interior. BB.28891.  $\times 4.4$ .







# PLATE 11

## *Sowerbyella sericea* (J. de C. Sowerby)

Upper Longvillian Substage, Alternata Limestone in Soudley quarry, 2 miles south-east of Church Stretton.

- FIG. 1. Internal mould of pedicle valve. BB.29064.  $\times 2.7$ .
- FIG. 2. Internal mould of pedicle valve. BB.29065.  $\times 1.9$ .
- FIG. 3. Latex cast of dorsal exterior. BB.29071.  $\times 2.3$ .
- FIG. 4. Latex cast of exfoliated ventral exterior. BB.29072.  $\times 1.7$ .
- FIG. 5. Internal mould of pedicle valve. BB.29066.  $\times 3$ .
- FIG. 6. Latex cast of dorsal interior. BB.29069.  $\times 1.7$ .
- FIG. 7. Latex cast of dorsal interior. BB.29067.  $\times 3.1$ .
- FIG. 8. Latex cast of dorsal exterior. BB.29070.  $\times 3$ .
- FIG. 9. Latex cast of dorsal interior. BB.29068.  $\times 3$ .

## *Sowerbyella sericea permixta* subsp. nov.

Nant Hir Group, mudstones on left bank of Nant Hir, 600 ft. north-east of Cefn-y-maes Farm.

- FIG. 10. Latex cast of dorsal exterior. BB.29097.  $\times 3.8$ .
- FIG. 11. Internal mould of pedicle valve. BB.29099.  $\times 3.4$ .
- FIG. 13. Latex cast of dorsal exterior. BB.29098.  $\times 3.6$ .
- FIG. 14. Latex cast of dorsal interior. BB.29096.  $\times 3.5$ .
- FIG. 15. Latex cast of dorsal interior. BB.29095.  $\times 7.8$ .
- FIG. 16. Holotype, latex cast of dorsal interior. BB.29093.  $\times 3.4$ .
- FIG. 17. Latex cast of dorsal interior. BB.29094.  $\times 6.0$ .

Glyn Gower Group, sandstones 1,100 ft. west of Y Fedw Farm.

- FIG. 12. Internal mould of pedicle valve. BB.29100.  $\times 3.3$ .

## *Sowerbyella musculosa* sp. nov.

Allt Ddu Group, sandstones below Pont-y-Ceunant Ash north of Y Garnedd Farm.

- FIG. 18. Latex cast of ventral exterior. BB.29092.  $\times 3.8$ .
- FIG. 19. Holotype, latex cast of ventral exterior. BB.29083.  $\times 3.2$ .
- FIG. 20. Internal mould of pedicle valve. BB.29086.  $\times 5$ .
- FIG. 21. Latex cast of ventral exterior. BB.29091.  $\times 4.8$ .
- FIG. 22. Holotype, internal mould of pedicle valve. BB.29084.  $\times 5.1$ .
- FIG. 23. Latex cast of dorsal interior. BB.29089.  $\times 6$ .
- FIG. 24. Latex cast of dorsal exterior. BB.29087.  $\times 5.7$ .
- FIG. 25. Latex cast of ventral interior. BB.29085.  $\times 5$ .
- FIG. 26. Latex cast of dorsal interior. BB.29088.  $\times 5.5$ .
- FIG. 27. Internal mould of pedicle valve. BB.28895.  $\times 4.3$ .



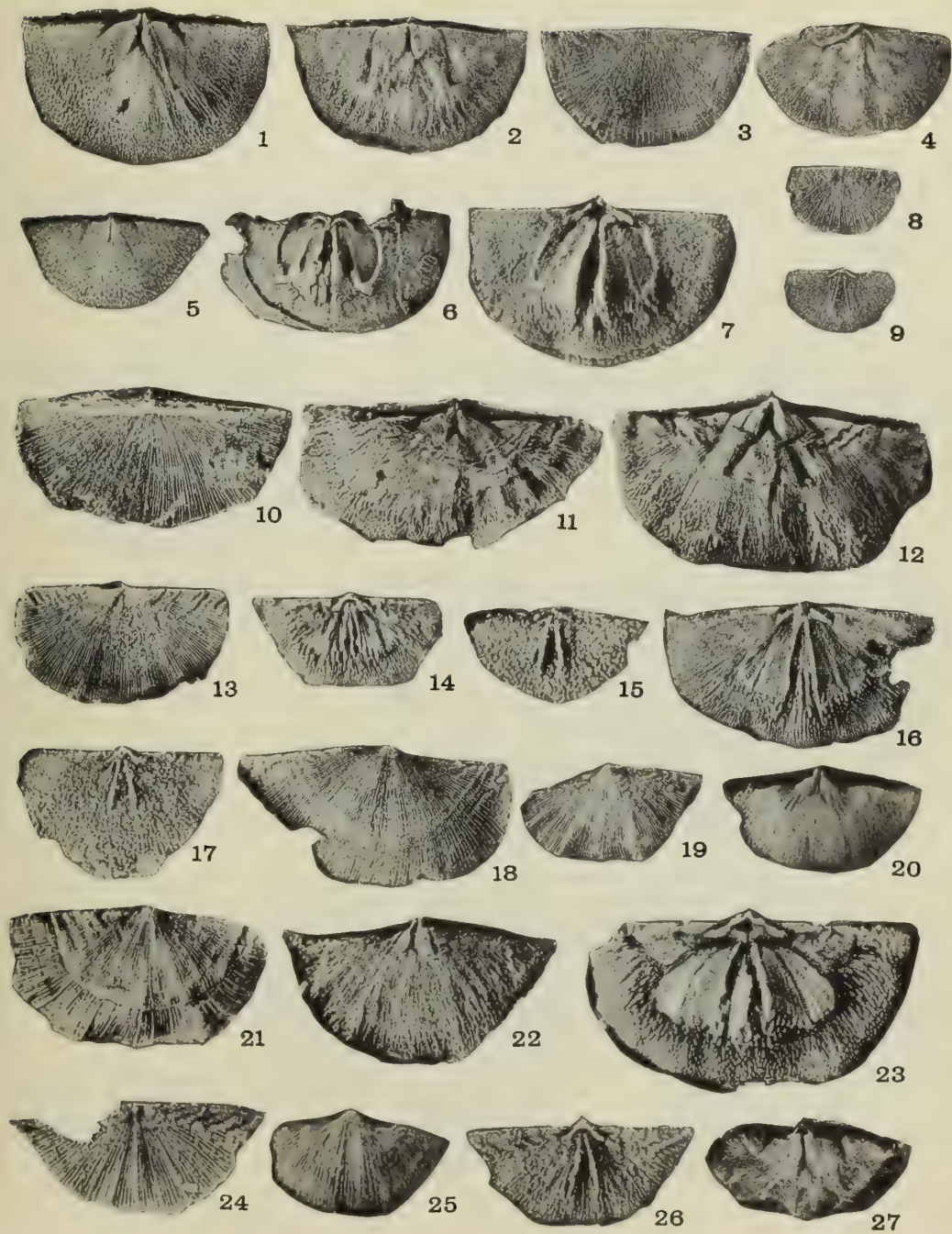




PLATE 12

*Sowerbyella soudleyensis* Jones

Lower Longvillian Substage, sandstones in old quarry on roadside south of Whittingslow, Shropshire.

- FIG. 1. Latex cast of dorsal exterior. BB.29081.  $\times 2.4$ .  
FIG. 2. Latex cast of dorsal exterior. BB.29082.  $\times 2.9$ .  
FIG. 3. Latex cast of dorsal interior. BB.29080.  $\times 4$ .  
FIG. 4. Internal mould of pedicle valve. BB.29077.  $\times 2.8$ .  
FIG. 5. Internal mould of pedicle valve. BB.29075.  $\times 3.9$ .  
FIG. 6. Internal mould of pedicle valve. BB.29073.  $\times 2.5$ .  
FIG. 7. Exfoliated exterior of pedicle valve. BB.29074.  $\times 2$ .  
FIG. 8. Latex cast of dorsal interior. BB.29079.  $\times 4$ .

*Eoplectodonta* cf. *rhombica* (M'Coy)

Gelli-grin Group, calcareous ashes in quarry at Y Garnedd Farm.

- FIG. 9. Internal mould of pedicle valve. BB.29123.  $\times 3.7$ .  
FIG. 14. Latex cast of dorsal interior. BB.29129.  $\times 2.3$ .  
FIG. 19. Latex cast of ventral exterior. BB.29125.  $\times 2.3$ .

Calcareous ashes 850 ft. west of Gelli-grin Farm.

- FIG. 10. Internal mould of pedicle valve BB.29122.  $\times 1.8$ .  
FIG. 11. Latex cast of dorsal interior. BB.29128.  $\times 2$ .  
FIG. 12. Latex cast of dorsal interior. BB.29130.  $\times 1.9$ .

Calcareous ashes 1,000 ft. west-south-west of Gelli-grin Farm.

- FIG. 13. Latex cast of ventral exterior. BB.29126.  $\times 2.5$ .  
FIG. 18. Latex cast of dorsal exterior. BB.29127.  $\times 1.8$ .

*Sericoidea* sp.

Gelli-grin Group, calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

- FIG. 15. Latex cast of ventral exterior. BB.29156.  $\times 5$ .  
FIG. 16. Internal mould of brachial valve. BB.29155.  $\times 5$ .

*Strophomena grandis* (J. de C. Sowerby)

Marshbrookian Stage, sandstones in quarry in Marsh Wood, Marshbrook, Shropshire.

- FIG. 17. Latex cast of ventral exterior. BB.29150.  $\times 1.3$ .  
FIG. 21. Latex cast of dorsal exterior. BB.29151.  $\times 1.6$ .

"Acton Scott", Shropshire.

- FIG. 20. Latex cast of dorsal interior. G.S.C.6897.  $\times 1.3$ .



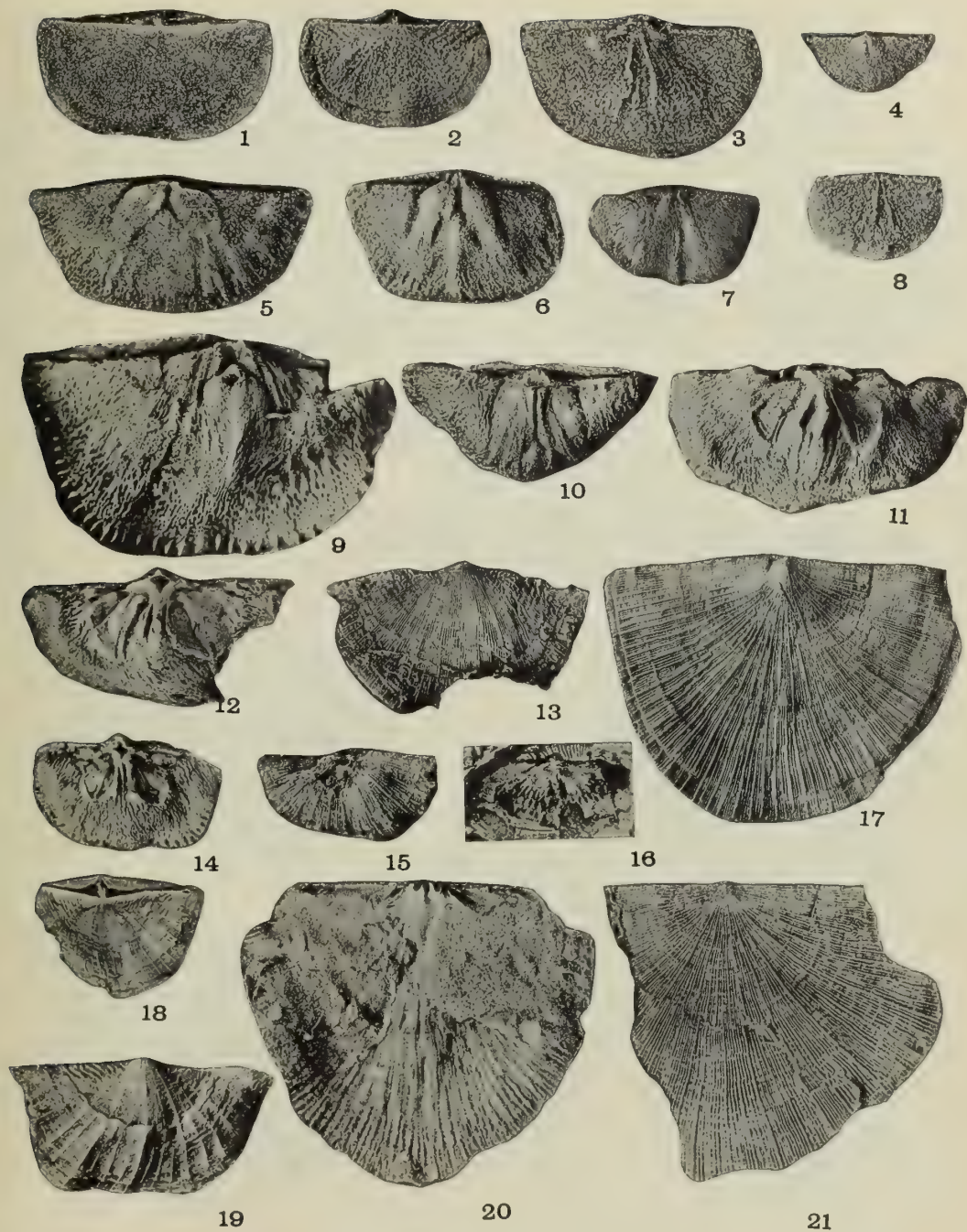




PLATE 13

*Strophomena* sp.

Gelli-grin Group, calcareous ashes in Ffridd Bach, south of Maes-meillion Farm.

FIG. 2. Latex cast of dorsal interior. BB.28887.  $\times 1.3$ .

Allt Ddu Group, sandstones 650 ft. east of Holy Trinity Church.

FIG. 3. Latex cast of ventral exterior. BB.29062.  $\times 1.4$ .

FIG. 4. Internal mould of pedicle valve. BB.29063.  $\times 1.4$ .

*Strophomena grandis* (J. de C. Sowerby)

Marshbrookian Stage, "Acton Scott", Shropshire.

FIG. 1. Lectotype, internal mould of pedicle valve. G.S.C.6823.  $\times 1.4$ .

*Glyptomena* cf. *osloensis* (Spjeldnaes)

Gelli-grin Group, calcareous ashes in quarry 1,450 ft. east-north-east of Y Garnedd Farm.

FIG. 5. Latex cast of dorsal interior. BB.29104.  $\times 3.5$ .

FIG. 6. Internal mould of pedicle valve. BB.29102.  $\times 2.1$ .

FIG. 8. Latex cast of ventral exterior. BB.29103.  $\times 2.2$ .

FIG. 9. Latex cast of ventral exterior. BB.29101.  $\times 2.1$ .

*Macrocoelia expansa* (J. de C. Sowerby)

Lower Longvillian Substage, siltstones on Gallt-yr-ancr 440 yds. north of west from Dyffryn.

FIG. 7. Latex cast of dorsal interior. BB.29117.  $\times 2$ .

FIG. 10. Latex cast of ventral exterior. BB.29118.  $\times 1.1$ .

FIG. 11. Latex cast of dorsal interior. BB.29112.  $\times 1.7$ .

FIG. 12. Latex cast of ventral exterior. BB.29114.  $\times 2.6$ .

FIG. 13. Internal mould of pedicle valve. BB.29113.  $\times 1.4$ .

FIG. 14. Internal mould of pedicle valve. BB.29116.  $\times 2$ .



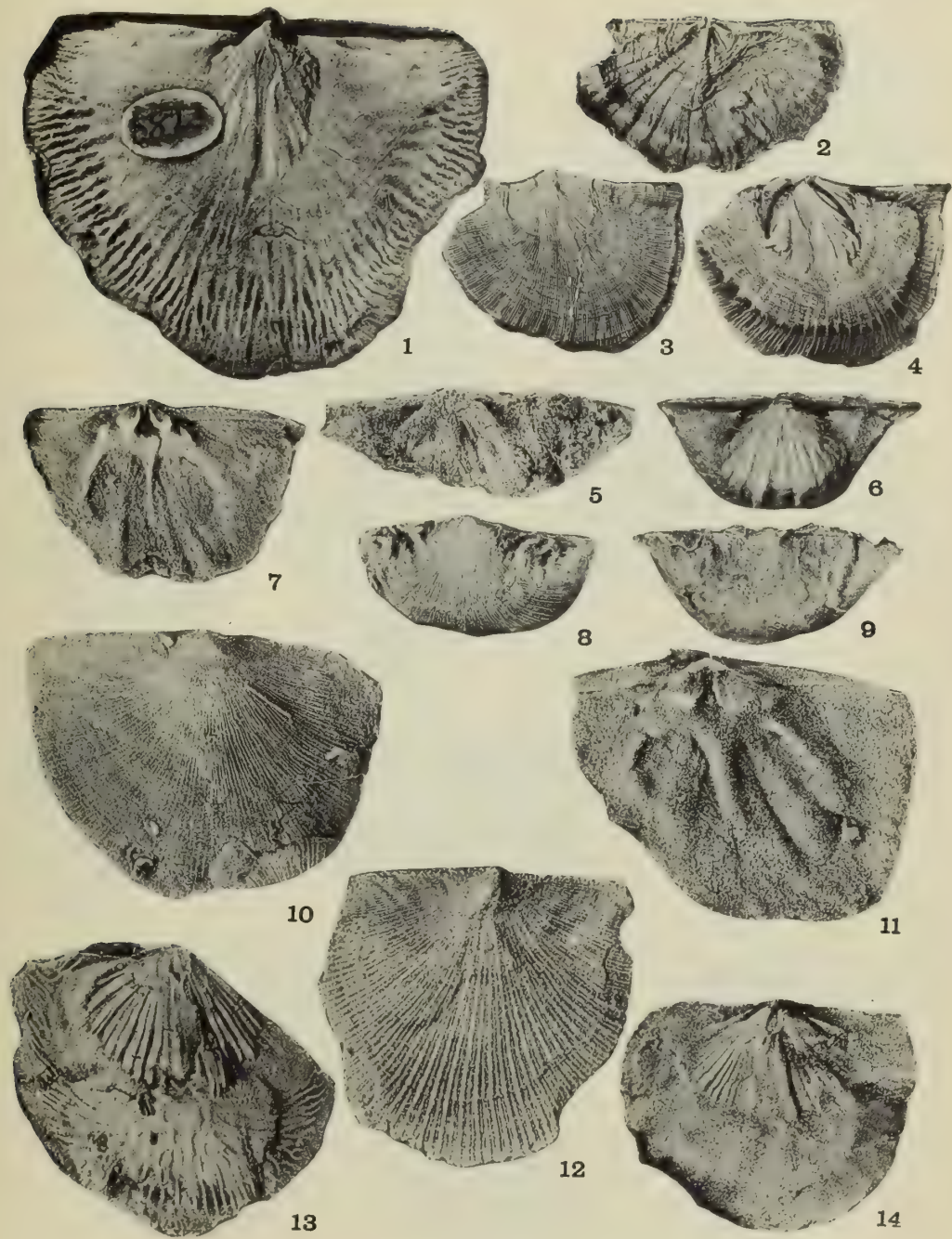




PLATE 14

*Macrocoelia expansa* (J. de C. Sowerby)

Lower Longvillian Substage, siltstones on Gallt-yr-ancr 440 yds. north of west from Dyffryn.

FIG. 1. Internal mould of pedicle valve. BB.29115.  $\times 1.7$ .

"Caradoc Sandstone, Meifod".

FIG. 2. Lectotype, internal mould of pedicle valve. G.S.C.6863.  $\times 1.2$ .

FIG. 5. Latex cast of ventral exterior. BB.29119.  $\times 2.5$ .

*Macrocoelia prolata* sp. nov.

Allt Ddu Group, sandstones underlying Pont-y-Ceunant Ash north of Y Garnedd Farm.

FIG. 3. Internal mould of pedicle valve. BB.29108.  $\times 2.7$ .

FIG. 4. Latex cast of dorsal interior. BB.29111.  $\times 5.6$ .

FIG. 6. Holotype, latex cast of ventral exterior. BB.29106.  $\times 1.4$ .

FIG. 7. Internal mould of pedicle valve. BB.29109.  $\times 1.8$ .

FIG. 8. Latex cast of ventral exterior. BB.29107.  $\times 3.2$ .

FIG. 9. Latex cast of dorsal interior. BB.29110.  $\times 3.9$ .

Sandstones 1,100 ft. south-west of Eglwys Anne.

FIG. 10. Latex cast of ventral exterior. BB.29105.  $\times 2.7$ .

*Hedstroemina* spp.

Nant Hir Group, mudstones on left bank of Nant Hir 600 ft. north-east of Cefn-y-maes Farm.

FIG. 11. Internal mould of pedicle valve. BB.29121.  $\times 1.8$ .

Glyn Gower Group, siltstones in wood immediately east of Cefn Bodig.

FIG. 12. Internal mould of pedicle valve. BB.29120.  $\times 3.8$ .



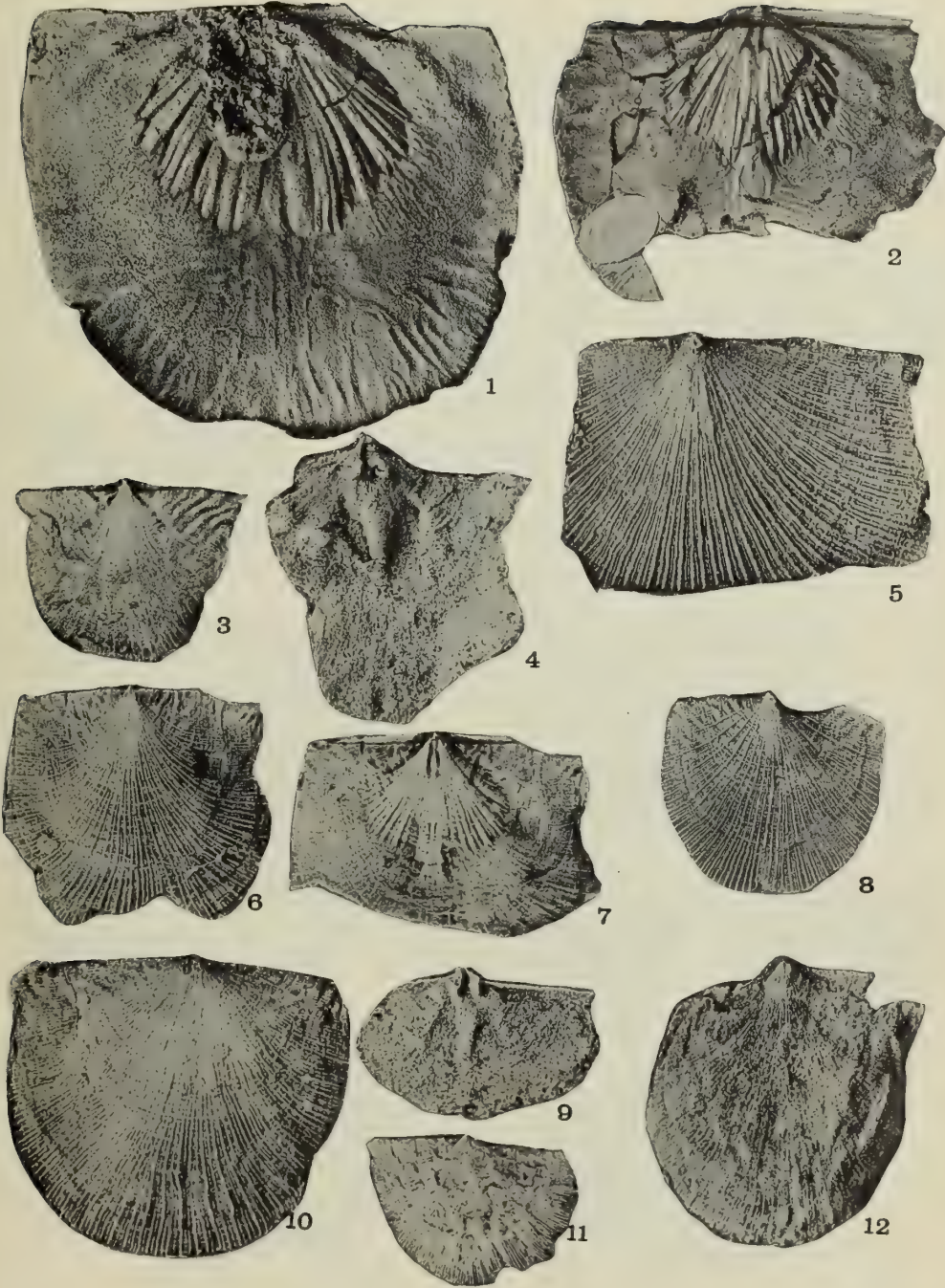




PLATE 15

*Leptaena ventricosa* sp. nov.

Gelli-grŷn Group, calcareous ashes on Creigiau Bychain.

FIG. 1. Latex cast of pedicle valve. BB.29048.  $\times 1.4$ .

Ashy mudstones 1,200 ft. east-north-east of Ty'n-y-wern Farm.

FIG. 2. Latex cast of pedicle valve. BB.29042.  $\times 2.5$ .

FIG. 3. Holotype, latex cast of dorsal exterior. BB.29044.  $\times 2.7$ .

Calcareous ashes 1,100 ft. just south of west of Gelli-grŷn Farm.

FIG. 4. Internal mould of pedicle valve. BB.29041.  $\times 2.6$ .

FIG. 5. Internal mould of pedicle valve. BB.29047.  $\times 2$ .

Calcareous ashes 2,600 ft. east of Pont-yr-onen Farm.

FIG. 6. Latex cast of dorsal interior. BB.29043.  $\times 2.3$ .

Calcareous ashes on Creigiau Bychain.

FIG. 9. Latex cast of dorsal interior. BB.29046.  $\times 2.6$ .

*Leptaena salopiensis* sp. nov.

Actonian Stage, loose blocks near Acton Scott Church, Acton Scott, Shropshire.

FIG. 7. Latex cast of dorsal interior. BB.29141.  $\times 2.1$ .

FIG. 8. Latex cast of dorsal interior. BB.29143.  $\times 2.1$ .

FIG. 10. Internal mould of pedicle valve. BB.29139.  $\times 1.8$ .

FIG. 11. Latex cast of ventral exterior. BB.29138.  $\times 1.9$ .

FIG. 12. Holotype, internal mould of pedicle valve. BB.29145.  $\times 1.6$ .

FIG. 13. Latex cast of ventral exterior. BB.29136.  $\times 2.1$ .

FIG. 14. Latex cast of dorsal exterior. BB.29140.  $\times 1.6$ .

FIG. 15. Internal mould of pedicle valve. BB.29137.  $\times 2.1$ .

FIG. 16. Holotype, latex cast of ventral exterior. BB.29144.  $\times 1.6$ .



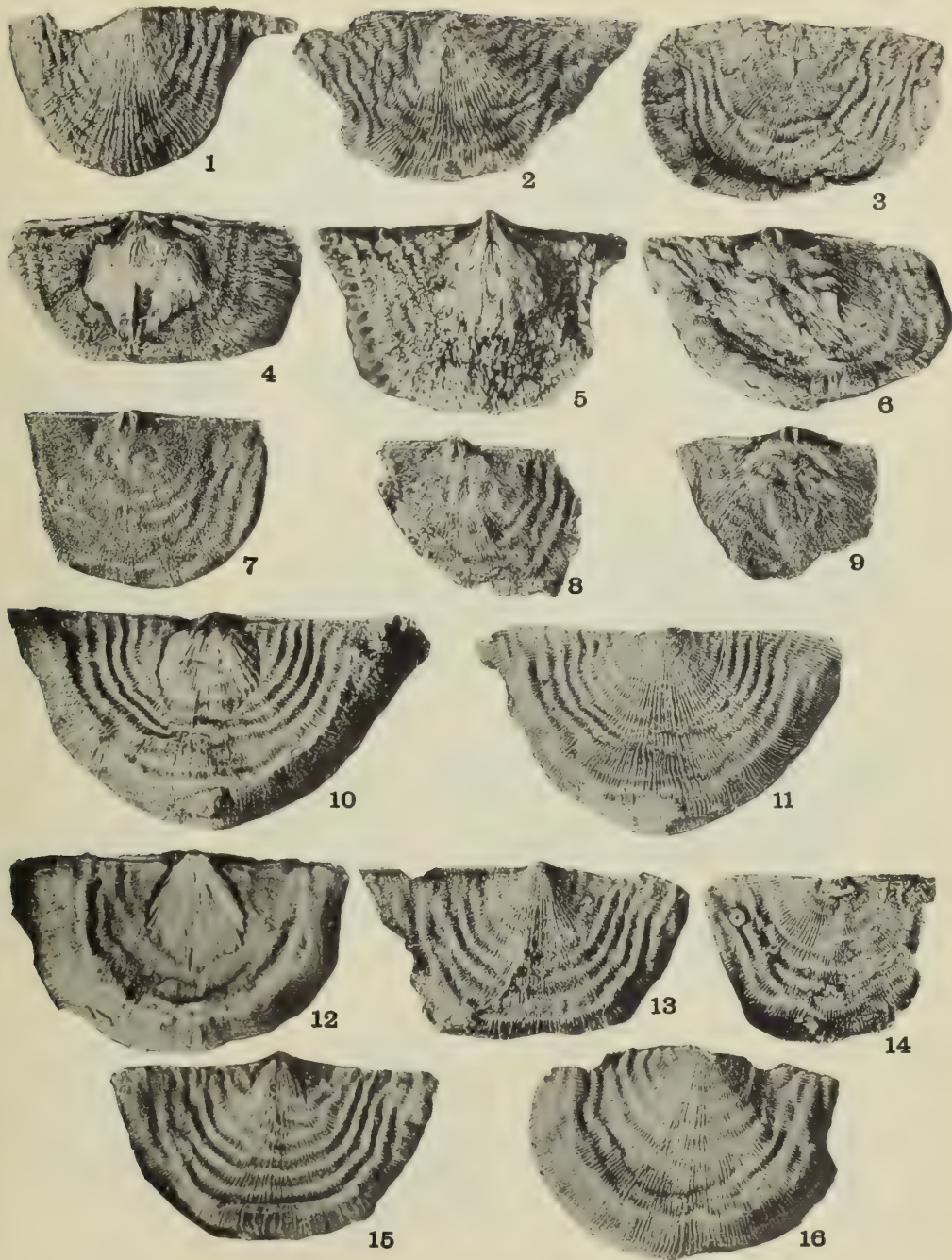




PLATE 16

*Kiaeromena* cf. *kjerulfi* (Holtedahl)

Allt Ddu Group, sandstones 450 ft. south of Pandy-isaf Farm.

- FIG. 1. Latex cast of dorsal interior. BB.29050.  $\times 2.8$ .  
FIG. 2. Latex cast of dorsal exterior. BB.29051.  $\times 2.5$ .  
FIG. 3. Latex cast of ventral exterior. BB.29052.  $\times 2$ .  
FIG. 4. Internal mould of pedicle valve. BB.29054.  $\times 2.1$ .  
FIG. 5. Internal mould of pedicle valve. BB.29053.  $\times 2.1$ .  
FIG. 8. Internal mould of pedicle valve. BB.29049.  $\times 1.8$ .

*Bellimurina incommoda* sp. nov.

Gelli-grin Group, calcareous ashes on Creigiau Bychain.

- FIG. 6. Internal mould of pedicle valve. BB.29057.  $\times 2$ .  
FIG. 10. Latex cast of ventral exterior. BB.29058.  $\times 2.4$ .  
FIG. 11. Latex cast of dorsal interior. BB.29059.  $\times 1.9$ .  
FIG. 12. Latex cast of dorsal exterior. BB.29060.  $\times 2.3$ .  
Calcareous ashes 1,000 ft. west-south-west of Gelli-grin Farm.  
FIG. 7. Latex cast of dorsal interior. BB.29061.  $\times 2$ .  
Calcareous ashes 650 ft. south-east of Bryn-briglas Farm.  
FIG. 13. Holotype, internal mould of pedicle valve. BB.29055.  $\times 2$ .  
FIG. 14. Holotype, latex cast of ventral exterior. BB.29056.  $\times 2$ .

*Rostricellula sparsa* sp. nov.

Allt Ddu Group, mudstones 1,100 yds. east of Pont-yr-onen Farm.

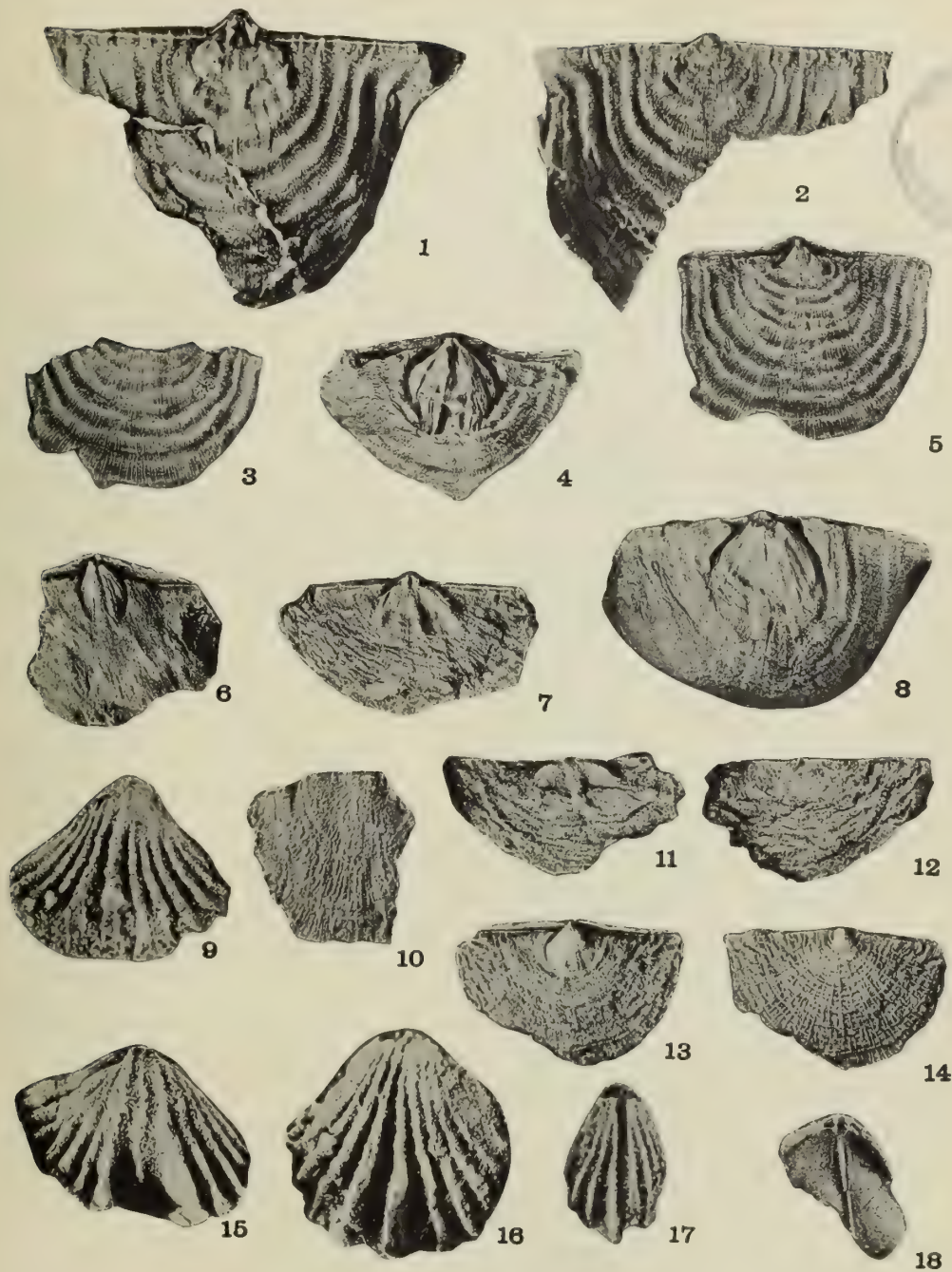
- FIG. 9. Latex cast of dorsal exterior. BB.28893.  $\times 7.6$ .  
FIG. 16. Holotype, latex cast of dorsal exterior. BB.29040.  $\times 9.4$ .  
Mudstones 320 yds. east-south-east of Glyn-bach.  
FIG. 15. Internal mould of pedicle valve. BB.28977.  $\times 5.3$ .  
FIG. 17. Internal mould of brachial valve. BB.28892.  $\times 7.0$ .

*Cyclospira* sp.

Gelli-grin Group, calcareous ashes in quarry at Y Garnedd Farm.

- FIG. 18. Latex cast of dorsal interior. BB.28976.  $\times 7.3$ .











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